

Chapter 1

Physiological, Molecular and Genetic Analysis of Abiotic Stress Tolerance in Tomato



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Abstract Tomato (*Solanum lycopersicum* L.) being most widely consumed vegetable is grown under diverse climatic conditions. It is exposed to episodes of abiotic stresses at critical stages and the potential yields are seldom realized. Abiotic stresses namely, high temperature, cold, drought, excess and low light, nutrient deficiency and toxicity and salinity limit production. Climate change is expected to further increase the incidence of various abiotic stresses. Under the circumstances it is rational to assess the adverse effects and devise means to overcome ill effects of diverse abiotic stresses on tomato. Tomato improvement efforts for desirable traits like yield and keeping quality have offered results. Evaluation of various tomato germplasm under different abiotic stresses has provided better insights into the existence of diversity in both cultivated and wild relatives. Though, substantial improvements have been made in understanding the abiotic stress tolerance mechanisms and gene discovery, the knowledge has not been exploited extent possible for development of tolerant commercial cultivars. Employing bioinformatics and molecular techniques there is remarkable opportunity for addressing complex breeding problems. Recent molecular tools have greatly helped the scientific community in assessing tomato germplasm for abiotic stress tolerance. Various physiological and biochemical analysis have been employed to understand the mechanisms operating during different abiotic stress tolerance. Using contrasting genotypes, many mapping and genetic studies have been conducted to identify genomic regions linked to abiotic stress tolerance. From these studies, various quantitative trait loci (QTLs) and genes have been identified. The markers could be valuable in improvement programs and for introgression of genes and QTLs from wild type species to *Solanum lycopersicum* using marker assisted selection (MAS). Many genetic engineering studies concerning transgenic and Crispr/CAS9 have demonstrated the association of various genes involved in imparting tolerance to abiotic stress in tomato. Sol Genomics, a database

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with genetic and genomic information on the plants belonging to Solanaceae family helps in providing sequence and marker related information which can be employed in MAS and genetic engineering. The opportunity for harnessing this information and devising strategies for tomato improvement for abiotic stress tolerance are discussed.

Keywords Abiotic stresses · Tolerance mechanisms · Quantitative Trait Loci · Transgenics · Breeding strategies · Marker assisted selection · Genomics

1.1 Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most widely consumed vegetables primarily due to its diverse consumption forms either as raw, cooked or various processed products. Its family Solanaceae also includes commercially important vegetables that are grown under diverse climatic conditions. Due to its demand for consumption in various forms, globally it is cultivated for both domestic needs and exports. Globally it is grown in an area of 5.03 million hectares with a total production of 180.76 million tons and productivity of 35.93 tons/ha (FAO 2019). Tomato crop is grown under diverse geographical regions either in open or under protected conditions. Two major tomato growing countries are China and India. Based on the extent of area and requirements it is harvested either manually or mechanically under intensive cultivation. The tomato fruit has diversity in color, shape and size. It is nutritionally important as it contains variety of phytochemicals. The fruit contains red color imparting pigment lycopene, which is a dominant antioxidant. Lycopene is important for maintaining eye health and reduces the incidence of cancer. The fruit also contains other carotenoids (β -carotene, phytoene, phytofluene) and phenolics (coumaric and chlorogenic acids, quercetin, rutin and naringenin). Vitamin C (ascorbic acid) in reasonable amounts is also present in tomato fruit. An alkaloid tomatine with fungicidal properties too is present. Hence, due its potential nutritional and health benefits, tomato is produced and consumed across the world.

1.2 Effect of Abiotic Stresses on Tomato Growth, Yield and Quality

Though tomato cultivation is widely adopted across the world in diverse agro-ecological regions, the potential yield is seldom realized due to episodes of many abiotic stresses. Abiotic stresses namely, high temperature, cold, drought, excess and low light, nutrient deficiency and toxicity and salinity limit crop production (Criddle et al. 1997; Cramer et al. 2011). Estimates of the effect of abiotic stress on global agriculture suggest that up to 70% of crop production is affected by ecological constraints (Boyer 1982; Cramer et al. 2011). Abiotic stresses are frequently interconnected, occurring either singly or in combination and cause morphological,

physiological, biochemical, and molecular changes in plants, reducing the development and production (Bulgari et al. 2019). Tomato requires accessibility of irrigation water throughout the crop growth cycle. It is sensitive to drought stress due to its succulent nature, and occurrence of deficit water stress during flowering and fruit set is very unfavorable. Deficit water stress caused reduction in yield to the extent of 11.69% and 30.60% under mild and severe water stresses, respectively. Conversely, fruit quality in terms of soluble sugars, total soluble solids, vitamin C contents, and fruit firmness was better under water stress (Hao et al. 2019b). The decline in plant height by 24%, stem diameter by 18% and chlorophyll concentration by 32% was observed in tomato under severe water stress condition. Consequently it resulted in 69% lower yield (Sibomana et al. 2013). The overall growth, flowering, yield and mineral nutrient uptake were significantly affected due to deficit irrigation (Ragab et al. 2019).

As a result of erratic rainfall the crops experience excess moisture stress and prolonged waterlogging situations. Such situations manifest into negative influence on crop growth and development. Waterlogging in tomato fields beyond two days leads to complete wilting and yield loss. Waterlogging induced anaerobic condition for 24 h resulted in 15% wilting and 40% yield loss (Hubbell et al. 1979). Flooding stress largely affected the physiology of tomato plants. Under stress tomato plants had lower photosynthesis rate, stomatal conductance, chlorophyll fluorescence, leaf water potential and chlorophyll content (Bhatt et al. 2015).

Maximum tomato rate of fruit growth and yield could be achieved at 25 °C (Adams and Valdes 2002). The critical nature of mean daily temperature on tomato was emphasized by Peet et al. (1997). The reduction in fruit number, per plant fruit weight and seed number was evident at mean daily temperature of 29 °C as compared to 25 °C. Thermal stress in tomato occurs at 35 °C. The exposure of plants to such high temperatures, results in physio-biochemical injury which adversely affect growth and yield (Rivero et al. 2004). High temperature stress during the growth of male reproductive part, leads to reduced fruit formation as a result of interruption in sugar and proline metabolism (Sato et al. 2006). Termination of flowers due to high temperature effect on bud formation and enlargement results in lower tomato yield (Peet et al. 1997; 1998; Sato et al. 2000). Increase in daily mean temperature adversely affects growth and productivity of tomato (Laxman et al. 2013, 2018).

Tomato is moderately sensitive to salinity. Salinity had its adverse influence on tomato root elongation, lateral root growth, reduced leaf, shoot height, stem diameter, photosynthesis and leaf chlorophyll content. At salinity equal and above 5 dS m⁻¹ the reduction in total yield was 7.2% per unit increase in salinity (Zhang et al. 2016). Since soil salinity influences seed germination and initial crop establishment, understating its influence is important for tomato production. Salinity level of 3.0‰ NaCl in Hoagland's solution affected germination of tomato seed. The germination process took longer and higher root/shoot dry weight ratio and Na⁺ content with reduction in K⁺ content were evident (Singh et al. 2012). At temperatures below 12 °C, the growth and development of tomato cultivars is adversely affected (Hu et al. 2006). Chilling stress damages tomato plants at prevailing temperatures between 0 and 12 °C depending on the duration of exposure (Adams et al. 2001). Thus, the

abiotic stresses have a greater bearing on overall physiology, growth, development and yield.

1.3 Growing Importance in the Face of Climate Change and Increasing Population

Tomato with desirable nutritional and health benefits is in great demand for domestic consumption and export. Increasing population driven demand poses a bigger challenge for sustainable tomato production. Further, there is a pressing need to manage the existing and future extreme weather events anticipated under climate change. The human induced increase in global surface temperature from 1850–1900 to 2010–2019 is likely in the range of 0.8 °C to 1.3 °C. Over the land surface the globally averaged precipitation has likely increased since 1950, with a quicker rate of increase since the 1980s. Currently observed variation in temperature events are projected to become more intense and last longer. The global temperature rise could be managed at 1.5 °C with determined efforts by cutting the emissions. These concerted efforts may prevent the most terrible climate impacts. However, as per the projections, under high emission scenario, the world may be warmer by 4.4 °C by 2100. Under such extreme scenarios the impacts would be devastating (IPCC 2021). Hence, there is an intense challenge of sustaining tomato production in the face of growing world's population on one hand and climate change on the other.

1.4 Limitations of Traditional Breeding and Rational of Genome Designing

Throughout the phenological development, tomato is subjected to a variety of abiotic stresses that adversely affect growth and yield. Among several approaches for sustaining and enhancing yields under adverse stress situations, identification of tolerant cultivars is of prime importance. Tomato breeding efforts for various desirable traits, especially yield and keeping quality, have been pursued in the past century employing pedigree method, hybridization, mass selection, and backcrossing. Such concerted efforts have led to improvements in tomato (Lucatti et al. 2013; Iqbal et al. 2019). Hybridization and pedigree selections have been the most important breeding techniques used in tomato improvement. The backcross method of breeding has been used to transfer desirable traits from wild species to cultivated varieties, among several other approaches (Sharma et al. 2019). Over the last seventy years, wild tomato species have been used in breeding programs to improve the cultivated tomato.

Development of tomato cultivars with enhanced abiotic stress tolerance is one of the most sustainable approaches to manage abiotic stresses. In this regard, considerable progress has been made to understand the stress tolerance mechanisms and gene discovery. Despite this there is no report of commercial cultivar tolerant to salt and/or drought stress. The literature on genetic variability, selection indices, important characteristics and genotypic responses to heat stress has been comprehensively reviewed by Hazra et al. (2007). The plant breeding programs need to translate the basic understanding gained from such studies into stress tolerant crop varieties using conventional and molecular tools. Tomato is a model plant for research in the Solanaceae family. The genomic sequence of tomato (*Solanum lycopersicum* L.) and its close wild relative (*Solanum pimpinellifolium* L.) are available (The Tomato Genome Consortium 2012; Aflitos et al. 2014). These advances encourage plant genomics and breeding studies for crop improvement.

Selection and breeding of tomato cultivars that can offer economic yield under abiotic stress situations signifies the lasting and balancing nature of this approach. An effective screening of the diverse genetic material is crucial for successful breeding strategy. The lack of a universal selection criterion for distinguishing tolerant and sensitive tomato accessions necessitates further research into identification of tolerance traits (Hirayama and Shinozaki 2010). The need for enhancing tolerance to abiotic stresses has necessitated the use of both traditional breeding techniques and marker-assisted selection. The evaluation of tomato germplasm under various abiotic stresses has provided better insights into the existence of diversity in both cultivated and wild relatives. However, utilization of diverse genetic resources in breeding tomatoes requires an efficient evaluation of germplasm using the phenotypic and genomic tools (Ayanan et al. 2019).

Following the breakthroughs in molecular biology and bioinformatics, breeding practices have improved (Caliman et al. 2008). These enhance the effectiveness of traditional plant breeding programs. The use of bioinformatics and molecular techniques can improve the screening of complex breeding problems (Ouyang et al. 2007). The narrow genetic basis in cultivated tomatoes for heat tolerance has triggered interest in exploiting tomato wild relatives, which have been sources for many abiotic and biotic stresses and yield related traits (Zhang et al. 2017a). Based on their ability to maintain photosynthetic rate and chlorophyll fluorescence under high temperature, Zhou et al. (2018) identified specific *S. pennellii* and *S. peruvianum* accessions as heat tolerant.

Current tomato breeding achievements are based on traditional breeding-genetic procedures, and limited improvements in introduction of useful traits into cultivars have been achieved. It's reasonable to believe that conventional breeding would not permit production to increase in the future (Fentik 2017). There has been significant development in molecular genetics and the application of molecular marker techniques. As a result, combining conventional breeding with modern plant biotechnology techniques such as marker-assisted selection and selection based on molecular markers could be useful tools for tomato breeding.

1.5 Response to Different Abiotic Stresses

Occurrence of abiotic stresses at critical growth stages not only severely limits productivity and yield but also quality of the produce. Under global climate change situations, abiotic stresses are of vital importance due to their widespread incidence. The occurrence of extreme high temperature and rainfall events are being reported across the world. Various abiotic stresses induce plant responses at different levels namely, morphological, physiological and biochemical/molecular alterations (Raza et al. 2019). At the morphological level, abiotic stress can cause altered shoot, root and leaf growth, as well as developmental changes that result in altered life cycle duration and fewer or smaller organs. Physiological activities such as photosynthetic rate, transpiration, respiration, assimilate partitioning to different organs within the plant, and mineral uptake is affected. At cellular level, membrane disruption, disorganized thylakoid structure, reduced cell size, stomatal guard cell function, alterations in cellular hydration and programmed cell death are manifested (Rao et al. 2016). At biochemical/molecular level, the effects include enzyme inactivation, production of reactive oxygen species (ROS), osmotic damage, changes in primary and secondary metabolite profiles, changed water and ion uptake or translocation and altered hormone concentrations (Etesami et al. 2021).

Maintenance of cell turgidity under stress is crucial for survival and to carry out metabolic activities. Plants have evolved various adaptive mechanisms to maintain positive turgor which mainly involves improving water relations and cellular level tolerance (Kapoor et al. 2020). Desired plant water status is sustained through mechanisms like alterations in phenology, maintaining positive turgor, and eventually sustaining cell metabolic activities despite decreased cell water potential. Cellular responses to stress include adjustments of the membrane system, modifications of the cell wall architecture, and alterations in cell cycle and cell division (Klutzn 2005). Therefore, two important relevant mechanisms are (a) improving water relations and (b) improving cellular level tolerance.

1.5.1 Roots Characters

Plants resort to several adaptive strategies through modifications in root characteristics. Such adaptations help to explore and access soil available water and maintain higher water use efficiency. Plants maintain positive turgor by taking up water from the deeper layers of soil (Robbins and Dinneny 2015). The roots act as crucial organ for meeting transpiration demand at a reasonably high leaf water status, given the condition that water is available in the rooting zone. Several root characters have relevance in stress adaptation. Studies have shown that genotypes with desirable root characteristics maintained cooler leaf temperature for longer period under water stress (White and Kierkegaard 2010). Nevertheless, these avoidance features help to maintain higher tissue water content under deficit moisture stress conditions. Such

adaptations facilitate plants to delay the immediate adverse effects of water stress. Hence, under severe deficit water stress conditions, the inherent tolerance characteristics are more important (Basu et al. 2016). Plants have exhibited many dehydration tolerance mechanisms under low tissue water potential by maintaining chloroplast integrity, membrane integrity and osmotic adjustment (Parkash and Singh 2020).

The importance of roots in accessing water from deeper layers of soil has also been the primary emphasis by the researchers. Roots, being below ground, respond to incidence of abiotic and biotic stresses in the soil and communicate with the aboveground plant parts via signaling pathways (Kim et al. 2020). The growth and development of plants is controlled by the root morphology and physiology through modifications in root to shoot transport of signaling molecules including hormones, proteins and RNAs and mineral nutrients (DoVale and Neto 2015). Roots being hidden in the soil are frequently exposed to multiple abiotic stresses occurring in the soil. Alterations in the shoot: root ratio is often detected when plants are subjected to various stresses (Fox and Fort 2019). Under drought, salt, or sub-optimal temperature stress, as well as some nutritional inadequacies or elevated levels of atmospheric CO₂, redistribution of metabolites from shoots to roots is frequently observed. Insufficient solar radiation or extra nutrients, on the other hand, usually result in a higher shoot-to-root ratio (Franco et al. 2011).

Roots have a greater ability to sense the physicochemical properties of the soil and change their development and performance, thus playing an important part in the plant's nutritional and development activities under abiotic stress (Kul et al. 2020). Roots are serving as the interface between the plant and the soil, hence more exposed to many abiotic stresses, especially drought, waterlogging and salt stresses than the aerial parts of the plant (He et al. 2018). Drought may cause a greater inhibition of shoot growth compared to root growth and in some cases; the absolute root biomass in drying soil may increase when compared to well-watered soils (Boudiar et al. 2020). Hence, the plants have developed various mechanisms to endure water or salt stress, including an altered shoot: root ratio.

Several studies have provided detailed insights into huge variations among tomato root traits (Table 1.1). The root characteristics like maximum root depth, total root length, root surface area, root volume, root diameter, root length density, root distribution pattern in the soil column, root to shoot ratio, root branching, root hydraulic conductance, root anatomy, root elongation rate, and hardpan penetrability. Intrinsic tolerance of roots plays a major role under stress condition (Sukeshini 2020). Hence, analysis of root phenotypes has revealed better understanding of root growth responses to a variety of environmental stimuli, as well as the extent of natural variation for root traits (Ristova and Busch 2014). Therefore, improving our understanding of the interactions between root functions and abiotic stress tolerance could have a significant impact on adaptation strategies.

Table 1.1 Root traits associated with different abiotic stresses in tomato species

Abiotic stresses	Root traits	References
Drought stress	Root length	Ron et al. (2013), Ghebremariam et al. (2013), Khan et al. (2014), Senthilkumar et al. (2017), Habib et al. (2019)
	Root biomass	Brdar-Jokanovic et al. (2014), Tron et al. (2015), Mahpara et al. (2018), Buhroy et al. (2017), Zhang et al. (2019), Zhang et al. (2020)
	Root/shoot ratio	Allerstorfer (2014), Niakan et al. (2014), Xiong et al. (2015), Zhang et al. (2020), Kamanga et al. (2020)
Salt stress	Root length	Almutairi, (2016), Tanveer et al. (2020), Habib et al. (2019), Altaf et al. (2020)
	Root biomass	Singh et al. (2012), Sajyan et al. (2018)
	Root/shoot ratio	Ebrahim et al. (2017), Parvin et al. (2019), Ladewig et al. (2021)
High temperature stress	Rootlength, Root biomass Root/shoot ratio	Keatinge et al. (2014), Haghighi et al. (2014), Shaheen et al. (2016), Ali et al. (2020)
Cold stress	Root length	Zhang et al. (2011), Subramanian et al. (2016), Wani et al. (2021)
	Root biomass	Ghorbanpour et al. (2018), Dezhabad et al. (2020)
	Root/shoot ratio	Klay et al. (2014), Altaf et al. (2021)

1.5.2 Heat Tolerance

As a result of global warming, coincidence of high temperature episodes with sensitive phenophases, leads to heat stress and is a major agricultural concern in many parts of the world. Heat stress is a vital limiting factor in agricultural output. There is a spike in air temperature over a threshold level for a period of time long enough to produce injury or irreversible damage to crop plants in general (Kumar et al. 2012; Lobell and Gourdji 2012; Gourdji et al. 2013; Teixeira et al. 2013). The extent of high temperature induced alterations in physiology, phenology, growth and yield depends on the duration, intensity and temperature increase over the threshold limits. The effects of heat stress on plants are very complex; resulting in denaturation of enzymes, disruption of metabolism activity, growth and development alterations, change in physiological functions and morphological structure (Mondal et al. 2013). Such alterations results in increased respiration, lower photosynthesis rate, closure of stomata, reduced chlorophyll fluorescence, lower chlorophyll content, membrane damage, ROS over production, and metabolic disruption upon exposure to heat stress (Hu and Zhu 2020). It could also alter the phenology, shorten the crop duration,

days to flowering and fruiting, hasten fruit maturity, ripening and senescence. These alterations result in reduced crop productivity and quality (Yu et al. 2019).

Tomato is cultivated in diverse agro-climatic regions across the world. It is very sensitive to high temperature (Camejo et al. 2005). Optimum mean daily temperature requirement is between 15–32 and 35 °C is considered as maximum threshold (Zhang et al. 2005). For growth, development and yield 40 °C is supra-optimum temperature (Morales et al. 2003). High temperature can undesirably impact seed germination, vegetative growth, pollination, flowering, fruit set, fruit weight and fruit quality (Foolad et al. 2005; Laxman et al. 2018). The gas exchange characteristics, photosynthesis, transpiration, stomatal conductance and photochemical efficiency of PSII were affected to a greater extent at peak flowering stage as compared to peak fruiting stage (Camejo et al. 2005, 2006; Laxman et al. 2013, 2014).

Previous studies have shown that the increase in daily mean temperatures adversely affect growth and productivity of tomato. The increase in temperature above the optimal, caused reduction in net photosynthetic rate, transpiration, stomatal conductance, and photochemical efficiency of PSII of five selected tomato genotypes during peak flowering and fruiting stages. The reductions were higher at peak flowering stage compared to peak fruiting stage (Laxman et al. 2013). The mild temperature also reduced in vitro pollen germination, fruit set percentage, fruit weight, number of leaves, number of branches, plant height, total dry matter accumulation, and harvest index in tomato plants. Concurrently, the number of trusses, flowers, and flower abortion also increased (Laxman et al. 2018). Antioxidant enzymes and the expression of HSPs/HSFs genes were found to be involved in the SIMAPK3-mediated heat stress response in tomato plants Yu et al. (2019). Mansy et al. (2021) studied six tomato lines, G1, G2, G3, G4, G5, and G6, under heat stress at the morphological, molecular, and cytological levels. The lines G2, G1, and G6 performed better in terms of morphological characters, vegetative development, fruiting, and yield.

In order to sustain productivity and quality under climate change situations, identification of tolerance source and development of suitable cultivars is the best adaptation strategy. For sustainable crop production under heat stress, two most imperative strategies could be followed: (a) introduction of tolerant cultivars, genetically modified or transgenic cultivars through molecular and biotechnological means along with conventional breeding approaches and (b) employing several agronomic management strategies for heat stress management under field conditions. As part of the strategy, coping up with high temperature stress under climate change conditions necessitates development of tolerant cultivars. This can be accomplished by breeding programs by exploiting the genetic capability of genotypes which are already temperature tolerant (Laxman et al. 2018). Bhattarai et al. (2016) examined a tomato cross to estimate combining ability and understand the genetic basis of tomato genotypes under heat stress. The genetic components and proportions studies showed that the heat tolerance was governed by non-additive gene action and is a dominant trait. The parental variance (V_r) and parent–offspring covariance (W_r) relationship (W_r-V_r) indicated that heat tolerance traits were governed by over dominance. Significant correlation occurred between yield and yield-attributing traits. Heterosis was high for yield and

most yield-attributing traits. Selection criteria should be to select heat tolerance traits in early generations followed by selection for yield.

The accurate and thorough understanding of reproductive key traits (flowers with exerted stigma, pollen viability, fruits set per cent and number of fruits per cluster), along with earliness (days to first fruit set) and yield traits (average fruit weight, pericarp thickness, number of fruits per plant and yield per plant) for heat tolerance of tomato is very essential. Insights of genetic architecture of the reproductive traits under heat stress might improve core understanding and might have applied significance. Therefore, new breeding lines and breeding strategies can be implemented under changing environmental conditions with special reference to elevated temperature (Archana et al. 2021).

Attempts have been made to evaluate the diverse tomato genotypes and assess the traits responsible for high temperature stress tolerance. Employing temperature induction response (TIR) technique, among the 52 tomato genotypes, 21 were identified as tolerant, 12 moderately tolerant and 19 genotypes as susceptible (Geeta et al. 2019). Such screening techniques that are simple and quick could be easily adopted in crop breeding programmes. In a study involving forty-nine diverse tomato genotypes, the tolerant genotypes exhibited lower reduction in photosynthesis rate, chlorophyll fluorescence transients, relative water content, membrane stability index and yield traits (number of fruits and fruit weight) with higher accumulation of osmolytes (Geeta 2020). Hence, breeding for high temperature tolerant crops needs high priority (Driedonks et al. 2016). In this endeavour, it is essential to fully characterize and identify genetic variation with respect to high temperature tolerance traits in the available germplasm before using them in a breeding program.

1.5.3 Cold Tolerance

Low temperature stress is categorized into chilling ($<20\text{ }^{\circ}\text{C}$) and freezing ($<0\text{ }^{\circ}\text{C}$) stresses. In addition to affecting the growth and development of the plants, cold stress significantly restrains the geographical distribution of plants (Liu and Zhou 2018). Tomato is an important thermophilic crop that is being cultivated in many areas worldwide (Yang et al. 2017). Adverse effects of cold stress on tomato caused reductions in yield and quality (Zhang et al. 2021). Cold stress adversely affects plant growth and development throughout the ontogeny of the tomato plant. During seed germination it delays the onset, reduces the rate, and increases the spread of germination events, resulting in poor stand establishment and crop performance. At later stages, cold stress results in reduced plant growth and development, delayed flowering, production of sterile pollen, low fruit set, and substantial reduction in fruit yield (Foolad and Lin 2000).

Plants must retain cell functionality and activity under cold stress, especially the stability of the cell membrane and the structure of the protein with biological activity, in order to survive in adverse environments. When plants are exposed to subzero temperatures, ice forms in the tissues. Plants with higher levels of active

ice nucleators in their apoplastic solution have a higher freezing point (Ritonga and Chen 2020). Developing cold-tolerant cultivars is one way to reduce the harmful consequences of cold stress. A cold-tolerant tomato cultivar should have the ability to germinate rapidly and uniformly, grow efficiently, produce flowers, and set fruit at low temperatures (Foolad and Lin 2001). At 4 °C low temperature, two wild *S. habrochaites* species, the IL LA3969 and its donor parent LA1777 were more cold tolerant than the IL's of recurrent parent *S. lycopersicum*, LA4024 (Liu et al. 2012).

Tomato plants treated with psychrotolerant bacteria isolates showed significant tolerance to chilling stress, as seen by reduced membrane damage and antioxidant enzyme activity, as well as proline synthesis in the leaves when subjected to chilling stress conditions. Their ability to promote germination, growth, and induce antioxidant capacity could help protect plants from chilling stress (Subramanian et al. 2016). As proposed by Liu et al. (2020), soluble carbohydrates influence tomato plant growth and development indirectly by serving as signal molecules in processes that increase tolerance to cold stress. Raffinose family oligosaccharides (RFOs) are an example and play an important role in cold stress tolerance. As a signal molecule in the activation of cold tolerance, galactinol plays an important role in RFO production as a critical limiting factor. Expression of galactinol synthase, *AnGolSI* in tomato enhanced cold tolerance and led to changes in the sugar composition of the seeds and seedlings.

As measured by free proline, membrane stability index, and PS II activity, transgenic tomato lines had a higher level of resistance to cold than normal plants (Parmar et al. 2017). Abscisic Acid (ABA) plays an important role in the induction of late embryogenesis abundant (LEA) gene expression (Lin et al. 2021). In plant vegetative tissues, exogenous ABA promoted the expression of certain LEA genes. ABA increased the expression of LEA genes during seed development and during abiotic stress exposure (Atayee and Noori 2020). The role of ABA in the up-regulation of LEA genes is considered to be one of the mechanisms that ABA increases freezing tolerance in tomato plants (Sah et al. 2016). Gibberellic acid (GA) is an important component of the plant's growth-control mechanisms and is altered in cold-stressed plants. GA has been observed to play a role in the expression of the CRT/DRE-binding factor gene, which provides cold stress resistance in plants (Atayee and Noori 2020). The lower expression of key GA metabolic genes, GA3ox1, GA20ox1 and GA2ox1 and GA3 treatment reduced the chilling injury index in tomato plants (Zhu et al. 2016).

1.5.4 Flooding Tolerance

The present weather patterns show occurrence of extreme rainfall events. Such extreme events are predicted to be more frequent under climate change conditions. The change in rainfall patterns would lead to excess and deficit moisture stresses at various stages of the crop growth. Excess moisture stress can alter the physiochemical properties of the soil which have an adverse effect on the plant growth and

development. The physical and chemical characteristics of soil, such as redox potential, pH, and oxygen content, are all affected by water logging (Pandey et al. 2021). Shortly after the soil is flooded, the respiration of roots and micro-organisms depletes the remnant oxygen and the soil environment becomes hypoxic (i.e. oxygen levels limit mitochondrial respiration) and later anoxic (i.e. respiration is completely inhibited) (Bailey-Serres and Voesenek 2008; Wegner 2010). Hence, the first constraint for plant growth under flooding is the immediate lack of oxygen necessary to sustain aerobic respiration of submerged tissues (Vartapetian and Jackson 1997; Striker 2012; Mignolli et al. 2021).

The earliest detectable physiological symptoms of flooding stress include decreased photosynthesis rate, stomatal conductance, transpiration rate, net assimilation rate and root hydraulic conductivity (Doupis et al. 2017). Ethylene directs the response of tomato to flooding stress; hypoxia that accompanies flooding causes an increase in the synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase in roots, as the expression of ACC synthase genes is induced and ACC oxidation is arrested in roots (Klay et al. 2018). Despite the fact that tomato plants can thrive in a variety of climates, they are one of the most vulnerable vegetable species to excessive soil wetness. Heavy rain combined with poor drainage causes water logging, which limits oxygen levels in the soil, resulting in plant mortality. Water stagnation in tomato fields for 2–3 days results in considerable crop loss and in some cases, complete plant death (Bhatt et al. 2015). Several studies have reported the antagonistic effect of excess moisture stress on plant growth and productivity. The findings of Ezin et al. (2010) revealed that the chlorophyll fluorescence and relative chlorophyll content act as a good criterion in the selection for flooding tolerance in tomato. Flood tolerant species are able to produce a lot of adventitious roots and sustain fruit yields. CLN2498E and CA4 genotypes were highly, and LA1421 moderately tolerant to flooding, and LA1579 was not tolerant to flooding. These flood tolerant genotypes could be used as good candidate lines in molecular breeding program to establish definite relation with chlorophyll fluorescence, chlorophyll content, yield and yield components. The effect of attenuated ethylene sensitivity in the Never ripe (Nr) mutant on leaf photosynthetic capacity of flooded tomato plants showed reduced ethylene perception in Nr plants. This was associated with a more efficient photochemical and non-photochemical radiative energy dissipation capability in response to flooding. The response was correlated with retention of chlorophyll and carotenoids in flooded Nr leaves. Therefore, besides its role as a trigger of many adaptive responses, perception of ethylene entails limitations in light and dark potential efficiency of PSII photochemistry; stomatal conductance; non-photochemical quenching; photosynthetic photon flux density, maximum rate of Rubisco-mediated carboxylation; intrinsic water use efficiency; actual photon yield of PSII photochemistry (De pedro et al. 2020).

When partially submerged, tomato plants undergo profound changes involving rearrangements in their morphology and metabolism; it markedly affects root respiration and halts root growth. Root sink disruption presumably causes sugars to accumulate in hypocotyls. As the availability of substrate (sucrose) increases, respiration is fueled creating a sucrose gradient that results in a sustained transport of carbohydrates

to the submerged hypocotyls (Mignolli et al. 2021). In this sense, remobilization of accumulated sugars in the hypocotyl could sustain root system growth resumption when flooding water recedes. Girdling and feeding experiments point to sucrose as the main carbon source for respiration. Consistently, submerged hypocotyls are characterized by high sucrose synthase activity, indicating that sucrose is cleaved and channeled into respiration (Mignolli et al. 2021).

Excess moisture condition can be overcome by identifying tolerant genotypes for sustainable tomato production (Ezin et al. 2010; Lin et al. 2016; Tareq et al. 2020; Mignolli et al. 2021). Inter-specific grafting approach to excess moisture condition has been reported in several studies (King et al. 2010; Keatinge et al. 2014; Bhatt et al. 2015; Bahadur Anant et al. 2015; Lin et al. 2016). Tomato and eggplant (*Solanum melongena* L.) plants differ in their resistance to flooding condition and have different physiological mechanisms to overcome flooding stress. Eggplant roots are relatively tolerant to flooding stress, survive better under excess water and exhibit better graft compatibility with tomato (Aganon et al. 2002; Black et al. 2003; Bhatt et al. 2015).

To overcome the deleterious consequence of flooding stress many studies emphasized on genetic modification approach through identification of gene and development of transgenic plants in tomato (Grichko and Glick 2001; Huther et al. 2016; De Pedro et al. 2020; De Ollas et al. 2021). As roots are the first organ to be affected by hypoxia, the ability to sense and respond to hypoxic stress is crucial. At the molecular level, therefore, fine-tuning the regulation of gene expression in the root is essential for hypoxia tolerance. Using an RNA-Seq approach, transcriptome modulation in tomato roots were examined and results suggested that the regulated genes identified are good candidate genes for hypoxia tolerance in tomato (Ivanchenko et al. 2020; Safavi-Rizi et al. 2020).

1.5.5 Water Use Efficiency

Water is essential for crop production across the world. Climate change triggered unpredictable rains cause frequent droughts. Such unusual rainfall patterns enforce crop cultivation under assured irrigation. The overdependence on ground water and other fresh water resources for crop production has resulted in depletion of freshwater available for irrigation. These circumstances, demand water-efficient crop growing practices. Enhancing agricultural water-use efficiency and sensible water use in crop production may help in realizing “more crop per drop” (Farooq et al. 2019). Water use efficiency (WUE) describes the intrinsic trade-off between carbon fixation and water loss that occurs in dry land plants because water evaporates from the interstitial tissues of leaves whenever stomata open for CO₂ acquisition. The transpiration efficiency of crop plants is generally low as they typically lose several 100-fold more water than the equivalent units of carbon fixed by photosynthesis (Bramley et al. 2013). With the increasing demand for sustainable water use and increasing agricultural productivity, the need to improve transpiration efficiency of crops has received much attention, although this trait may not be beneficial in all water-limited environments.

WUE may be estimated as the ratio between net photosynthesis (Pn) and transpiration (E), which is known as instantaneous water use efficiency (physiological index) (Polley 2002). The ratio between Pn and stomatal conductance (gs), is known as intrinsic water use efficiency (Lei 2018). And the ratio of dry matter accumulation over time to the amount of water transpired is known as biomass/ yield water use efficiency. A large diversity in WUE has been reported among different crops and genotypes. The limited water availability situations for crop production could be managed through increase in WUE. Wild tomato species are genetically diverse and exhibit a range of tolerances to one or more abiotic stresses. Wild species, including *S. habrochaites*, have been reported to exhibit increased WUE when compared to cultivated tomato (Zsogon et al. 2017). Deficit irrigation resulted in higher water use efficiency compared to full irrigation in case of fresh and dry tomato fruits (Djurovic et al. 2016). Changes in WUE under full and deficit irrigation conditions were also reported by Topcu et al. (2007), Patane and Saita (2015), Wang et al. (2015). The limited water availability situations for crop production could be managed through increase in WUE. Wild tomato species are genetically diverse and exhibit a range of tolerances to one or more abiotic stresses. Tomato yield and WUE increased asymptotically with irrigation amount before approaching their plateau when the irrigation amount reached 90% and 70% of accumulative evaporation, respectively. While the yield was positively related to fruit size and negatively to soluble solid content, this was independent of WUE (Liu et al. 2019). WUE significantly increased under non-loamy soil while not in loamy soil. Under regulated deficit irrigation (RDI) WUE increased significantly and was beneficial if RDI was applied to tomato in non-loamy soil, since reductions in yield were lower and water use efficiency higher (Lu et al. 2019). Subsurface drip irrigation (SDI) with air injection act as a useful strategy to the reduce evapotranspiration (ET) and the improvement of WUE of tomato (Wang et al. 2020a).

To address nutrient deficiencies by root due to water deficit condition, foliar fertilization with water soluble Tecamin flower®, a product containing chemicals were utilized to evaluate impacts of foliar application at 0 or 2.5 ml/l and deficit irrigation (50 or 100% of field capacity) in tomato (*Solanum lycopersicum* L.) cvs. Bobcat, Finenss and Hadeer. The plant treated with 2.5 ml/l Tecamin flower® produced the highest vitamin C content, total soluble solids, titratable acidity, fruit firmness, total yield, WUE and the lowest pH. Foliar application of Tecamin flower®, regardless of cultivar, improved production, fruit quality and WUE of tomato under normal and water deficit conditions and played a role in alleviating the negative impact of water deficit (Al-Shammari et al. 2020). Hence, studies on response of tomato genotypes and assessment of WUE not only helps in understanding the diverse physiological response of tomato genotypes to water stress but consequently in realizing sustained yields under water limiting conditions.

1.5.6 Nutrient Use Efficiency

Nutrient use efficiency (NUE) is a critically important concept for evaluating crop production systems and can be greatly determined by fertilizer management as well as soil- and plant-water relationships. NUE is a measure of how best plants utilize the available mineral nutrients in the soil as well as from applied source of nutrients in the form of fertilizers. It can be defined as yield (biomass) per unit input (fertilizer, nutrient content) (Fixen et al. 2014). It is one of the complex traits: it depends on the ability of plant to take up nutrients from the soil, but also on transport, storage, mobilization, usage within the plant, and even on the environment. Improved NUE is not just a prerequisite for advancing crop production into relatively low soils, but it is also a strategy to reduce inorganic fertilizer consumption (Reich et al. 2014). NUE is of particular interest as a major target for crop improvement.

The tomato genotype, LA-2157 having ability to use nitrogen efficiently in terms of production of biomass per unit of applied nitrogen under both high nitrogen source and low nitrogen source media was identified. It confirms the availability of source for exploitation in future tomato breeding programmes (Jasmitha 2020). Evaluation for absorption and utilization of phosphorus in three tomato genotypes at different levels of P_2O_5 showed that the genotype, Globonnie had greater efficiency of phosphorus absorption and utilization applied at lower doses (Marques et al. 2018). An anthocyanin-free tomato genotype H957 could tolerate lower phosphorus concentration by utilizing internal P with better efficiency rather than by better absorption of external phosphorus (Lee et al. 1998). The genotypes, *Solanum pimpinellifolium*, *Solanum peruvianum*, *Solanum galapagense*, *Solanum arcanum*, PKM-1, Arka Samrat were identified having higher phosphorus acquisition efficiency (Soumya 2020).

The development of new strategies to overcome production failure and the improvement of NUE are dependent on management practices. Quantifying the true status of nutrient use efficiency in agriculture however remains, difficult as reliable farm level data are not widely available (Dobberman 2007). Abiotic stresses and nutrient deficiencies in the soil are two important environmental factors that affect plant growth, productivity, and quality. Earlier studies suggested that grafting approach act as a tool to improve NUE in tomato plants. Where, selection criteria for the breeding of rootstocks help to enhance NUE of elite tomato cultivars under a wide range of growth (root) environment conditions (Venema et al. 2011). Grafting studies indicated that rootstocks affect leaf macronutrient content and enhance nutrient uptake and NUE (Rivero et al. 2005; Leonardi and Giuffrida 2006).

1.5.7 Drought Tolerance

Moisture deficit stress has a major adverse effect on plant growth and development in terms of alterations in physiology, growth, metabolism and production. Extent

of damage varies with the level of plant tolerance (genotype), duration, timing and intensity of the stress. Moisture stress affects plant water relations, reduced water content, stomatal movement, limits gaseous exchange, reduces transpiration, reduces carbon assimilation (photosynthesis) rates, mineral nutrition (uptake and transport of nutrients) and metabolism. It leads to a reduction in the leaf area and thus altered assimilate partitioning among the different parts of plants.

Tomato is sensitive to drought stress at all stages of plant growth and development. In terms of productivity, the transplanting, flowering and fruit setting phases have been considered to be the most susceptible phases. Tomato plants growing under moisture stress are generally associated with slow growth, and in severe cases, dieback of stems and death. Such plants are more susceptible to disease and less tolerant of insect feeding. The germination and initial seedling establishment are the first to be adversely affected under scarcity of water (Hamayun et al. 2010). Deficit moisture at germination stage will delay and reduce germination and under severe conditions, may even completely hinder the seed germination. Reduction in seed germination to an extent of 40–60% can be observed under deficit moisture conditions (Ayaz et al. 2015).

Drought stress in tomato is also associated with increased salinity levels which reduce seed germination. It affects both cell elongation and expansion during plant growth and development resulting in reduction in plant height. Under severe water deficiency, cell elongation can be inhibited by interruption of water flow from the xylem to the surrounding elongating cells (Nonami 1998). Water deficit stress caused impaired mitosis, cell elongation and expansion resulting in reduced growth and yield traits (Hussain et al. 2008). Plant height could reduce up to 58% under severe stress conditions (at 35% moisture of field capacity). Low moisture stress condition reduces tomato growth cycle by accelerating different growth and development stages. With the onset of drought stress, plant developmental phase is stimulated to shift from vegetative to reproductive phase. Relative water content (RWC) and electrolyte leakage are the indicative of metabolic activities within plants and are used for evaluation of plant tolerance to different abiotic stresses including drought. Under stress conditions, RWC decreases and electrolyte leakage increases with increasing stress levels (Ullah et al. 2016).

Tomato plants require a consistent supply of water throughout the growing season in order to achieve maximum quality and output. Tomato plants should be irrigated frequently with small amounts of water and need to receive water between 400 and 600 mm during the growth period. The plants should not be allowed to consume more than 40% of the available moisture in the soil. Water stress at an early stage of development (20 days) is more inhibitory than at a later stage (30 days) (Shamsul et al. 2008). Further, photosynthesis is hampered by stomatal closure and metabolic damage caused by a lack of water. Plant hormones play a critical role in the internal signaling network, and regulate plant growth and development in response to external signal cues (Liu and He 2017). Under water stress conditions, concentrations of ABA, hormone responsible for stomatal closer under water stress condition, can increase up to 50 times. Higher levels of Zeaxanthin epoxidase (ZEP) transcript levels, an

important component of ABA synthesis which catalyzes the synthesis of violaxanthin, were observed in root but not in leaves of tomato plants during drought stress. They initiate signal transduction under stress conditions and further regulate stomatal behavior and reduce transpiration rate by closing stomata (Thompson et al. 2000). ABA also regulates root-shoot ratio of tomato plant and stimulates higher root growth as compared to shoot under water stress condition (Sharp et al. 1988).

Water stress stimulates excessive production of ROS. The increased activity of antioxidant enzyme defense system, superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT), is an adaptive response of plant to drought tolerance. In tomato plants, the activity of SOD was more correlated to drought stress than those of ascorbate peroxidase or catalase (Aghaie et al. 2018). Proline accumulation is a significant response of plants under drought stress conditions. PEG induced drought stress has shown to enhance endogenous proline concentrations in tomato calli (Shtereva et al. 2008). This osmolyte acts as a scavenger of OH^- radical and plays an important role in osmotic adjustment during oxidative stress (Anjum et al. 2000). Further, Proline assists in sustained root growth under water stress condition. It accumulates in root growing zone and increases the activity of enzyme such as xyloglucan endotransglycosylase (XET) and accelerates cell elongation by cell wall loosening (Hartung et al. 1999) inducing root growth under drought stress.

Drought stress severely hampers the gas exchange characteristics of crop plants and this could be due to decrease in leaf expansion, impaired photosynthetic machinery, premature leaf senescence, oxidation of chloroplast lipids and changes in structure of pigments and proteins (Menconi et al. 1995). Under mild drought stress, inhibition of photosynthesis is due to stomatal closure caused by the imbalance between light reaction and Calvin-Benson cycle as a consequence of limited CO_2 diffusion into the leaf (Chave et al. 2009). Under severe water stress conditions damage to photosystem, inhibition of Rubisco and other enzyme activities lead to decrease in photosynthesis rate (Yuan et al. 2016). The net photosynthetic rate declines distinctly with the decrease in transpiration rate and stomatal conductance with the prolonged water stress. Further, the stomatal length and stomatal width decreases with increase in stomatal density during the stress conditions (Hao et al. 2019a). With the increase in the degree of drought stress, chlorophyll fluorescence characteristics gradually decrease, due to the closure of the PSII reaction center, limiting electron transfer and reducing the light energy available for actual photochemical reactions in the PSII reaction center leading to reduced photosynthetic rate (Table 1.2).

During drought stress conditions, several genes are activated which lead to physiological and metabolic changes against the stress perceived. Drought tolerance is a polygenic trait involving several genes via a complex mechanism. Drought induced genes are regulated by a specific signal transduction pathway which activates transcription factors. These activated genes are involved in protection with creation of efficient antioxidant system, water channels/ transporters, key enzymes for osmolyte biosynthesis (proline, sugars), protection factors for new molecules (LEA proteins, chaperons), ABA biosynthesis, etc. (Shinozaki and Shinozaki 2007) (Table 1.3).

Table 1.2 Impact of drought on photosynthetic parameters in tomato plants

Photosynthetic parameter	Impact	References
Net CO ₂ assimilation rate	Decrease	Rao et al. (2000)
Transpiration rate	Decrease	Hao et al. (2019a)
Stomatal conductance	Decrease	
Intercellular CO ₂	Increase	Rao et al. (2000), Hao et al. (2019a)
Transpiration	Decrease	Hao et al. (2019a)
Stomatal limitation	Increase	Liang et al. (2020)
F _v /F _M	Decrease	Liang et al. (2020)
NPQ	Initially increase later decrease	Liang et al. (2020)
Rubisco (rbcS)	Decrease	Bartholomew et al. (1991)
Chlorophyll content	Decrease	Ghorbanli et al. (2013)

Table 1.3 Characteristics of genes potentially involved in stress response in tomato

Gene	Characteristics/Description	Function	References
<i>SIGATA17</i>	GATA transcription factor	Regulate the activity of the phenylpropanoid biosynthesis pathway	Zhao et al. (2021)
<i>JUB1</i>	NAC transcription factor	Activation of <i>DELLA</i> and the stress-related genes <i>DREB2</i> and <i>DREB1</i> , reduced ROS levels	Thirumalaikumaret al. (2018)
<i>SL-ZH13</i>	Zinc finger-homeodomain proteins	Increased antioxidant activity	Zhao et al. (2019)
<i>HsfA1a</i>	heat-shock transcription factor	Activate ATG genes and induce autophagy	Wang et al. (2015)
<i>AnnSp2</i>	Annexin; Calcium-dependent phospholipid-binding proteins	ABA synthesis and the elimination of ROS	Ijaz et al. (2017)
<i>BES1</i>	BES1 transcription factor	BR signaling transduction and the elimination of ROS	Wang et al. (2020c)

The limited water availability situations for crop production could be managed through increase in WUE. Wild tomato species are genetically diverse and exhibit a range of tolerances to one or more abiotic stresses. Wild species of *S. pimpinellifolium*, *S. pennellii*, *S. habrochaites*, *S. chmielewskii*, and *S. cheesmanii* are shown to have tolerance to drought stress and they can be suitably exploited for transfer of genes to cultivated species (Solankey et al. 2015). The *S. chilense* is five times more tolerant to wilt than other cultivated tomato. *S. habrochaites* and *S. pennellii* have been reported to exhibit increased WUE when compared to cultivated tomato. These

species possess well-developed, longer, primary roots and more extensive secondary roots than cultivated tomato and have thick, round, waxy leaves having acyl-sugars in the trichomes (Easlon et al. 2009; Nicoleta and Nedelea 2012).

1.6 Breeding for Abiotic Stress Management in Tomato

1.6.1 Salt Stress

Salinity in tomato affects different aspects of the physiology and biochemistry of plants and thus significantly reduces yield. There are comparatively more salt tolerant wild relatives of tomato. Because of the large number of genes involved in salt tolerance, it is difficult to enrich elite lines with genes from wild species that confer tolerance. If it is possible to unravel the molecular markers tightly linked to the genes governing salt tolerance, their favourable alleles could be selected in segregating populations using tightly linked markers and eventually incorporated into salt-tolerant cultivars.

Tomato wild relatives are important sources of genes and salt tolerant traits. Wild relatives such as *S. peruvianum*, *S. chilense*, *S. habrochaites*, *S. pimpinellifolium*, *S. cheesmaniae*, and *S. pennellii* are known to be less sensitive to saline growth conditions. The QTL analysis of salt tolerant accessions of *S. pimpinellifolium* and *S. cheesmaniae* led to the discovery of highly significant QTLs (>40%) on chromosome 7 that contribute to salt tolerance in terms of Na⁺ and K⁺ concentration. The candidate genes of tomato *LeNHX3* gene and two other high affinity potassium transporters (*HKT1*) are located on chromosome 1 and chromosome 7, respectively (Villalta et al. 2008). The tomato *LeNHX3* gene contributed to higher accumulation of leaf Na⁺ and the QTLs of *S. cheesmaniae* contributed to build up higher levels of Na⁺ and/or lower K⁺/Na⁺ ratio in leaves. The markers linked to such contributing alleles can be used in marker assisted introgression. The genome-wide markers available now due to advances in genomics can be used for mapping QTLs contributing to salt tolerance using linkage analysis or association mapping (AM) studies. Using AM studies, two important genes of *S. pimpinifolium* namely *AVP1* encoding vacuolar H⁺-pyrophosphatase and *LeDREB1A* were identified as critical genes for salinity tolerance (Rao et al. 2015).

The selections were made for salinity tolerance at germination, seedling establishment and reproductive stage from the progenies of cross between *S. cheesmaniae* and tomato cultivar *S. lycopersicum*. The selected progenies were tested for survival and fruit production in salinized solution culture experiments and greenhouse trials. The plants selected from the F₂ and successive backcrosses to the cultivar survived and produced fruit when irrigated with up to 70% sea water in the sandy soil culture trials, whereas tomato cultivar did not survive in saline conditions (Shah et al. 2008). The over expression of a known multiple stress responsive gene proline-, lysine-, and

glutamic-rich type gene SpPKE1 isolated from *S. pennellii* enhanced the salt tolerance in tomato. Therefore, SpPKE1 and *S. pennellii* could be an important candidate gene and a species for molecular breeding of salt-tolerance in tomato (Li et al. 2019).

1.6.2 Heat Stress

Tomato is sensitive to heat stress. The vegetative and reproductive growth of tomato is impacted by heat stress which can lead to significant total yield loss. Therefore, it is imperative to identify heat tolerant genotypes and develop heat tolerant cultivars. There is significant genetic variability in tomato germplasm with regard to heat tolerance (HT) that can be harnessed to breed heat tolerant cultivars. The essential components of breeding heat tolerance in tomato are screening germplasm, trait breeding for target traits and MAS. Screening germplasm for HT is a critical component. The screening can be carried out under controlled environment conditions such as phytotrons, growth chambers, and greenhouses. However, the applicability of the findings of controlled environment conditions needs to be tested and verified in field conditions. Alternatively, screening at field conditions can also be initiated in parallel to complement the findings of controlled environment studies. The GxE interaction in the field conditions could also play an important role in response to heat stress. Therefore, it is always desirable to screen germplasm in multi-environment conditions including seasons and locations.

The trait breeding strategy may have to be adopted to enhance HT in cultivars. The traits with high heritability should be targeted to achieve better genetic gain in terms of HT. Several studies have focused on morphological, reproductive, physiological and biochemical traits. In general, these studies have focused on male reproductive traits (pollen viability, pollen number and anther dehiscence), female fertility traits (stigma receptivity and seed set after artificial pollination), biochemical traits (soluble sugars, osmolytes, flavonoids and pectins), membrane thermo stability and physiological traits (chlorophyll fluorescence, canopy temperature and transpiration rate) (Ayenan et al. 2019).

Deploying MAS is critical for improving the accuracy and efficiency of HT breeding. This depends on the availability of reliable marker and trait linkage or association. In this regard, advanced backcross populations and chromosome segments substitution lines have been used to exploit genetic variability that exist in non-cultivated tomato species. Several bi parental mapping studies have been conducted so far. The genetic basis of variation in HT of a tolerant line Nagcarlang was investigated previously in a F2 mapping population under continuous mild heat conditions. Then the QTLs were identified for a number of traits related to reproductive success including a highly significant QTL which accounted for 36% of phenotypic variation in the population for pollen viability (Xu et al. 2017). The A meta quantitative trait loci (MQTL) analysis of four mapping experiments led to the conclusions that QTLs associated with heat tolerance traits might show pleiotropic effects on HT or tight linkage of QTLs of HT traits which was evident from the co-localization of QTLs

(Ayenan et al. 2019). Aside from fruit set percentage, fruit weight is also negatively impacted due to heat stress.

Therefore, understanding basis of negative association between fruit weight and thermo-tolerance is required. This aspect of fruit development requires attention since the overall improvement of yield under heat stress will depend on fruit number and fruit size. In an association mapping experiment, six yield-related traits including flower earliness, number of flowers per inflorescence, fruit set, number of fruit per plant, fruit weight and yield per plant were studied (Ruggieri et al. 2019). A total of 15 common markers associated with these traits were identified. The most relevant associations co-localized with genes involved in the floral structure development, such as the style 2.1 gene, or with genes directly involved in the response to abiotic stresses. These promising candidate genes could be used as potential genes to improve tomato cultivar performance under high temperatures.

1.6.3 Drought Stress

There is great deal of genetic variation in tomato for drought stress resistance mostly in wild relatives. Among the tomato wild species, *S. pennellii*, *S. chilense* and *S. sitiens* are known drought-adapted species. The *S. pennellii* has been used as an experimental model to gain deeper insights in to the underlying molecular mechanisms of drought adaptation and tolerance in tomato (Atarés et al. 2011). The availability of genome sequence, introgression library and backcross inbred lines has assisted in the identification of mechanisms involved in stress tolerance including other traits of importance.

The physiological level changes observed between *S. pennellii* and cultivated tomato demonstrated that *S. pennellii* exhibits reduced stomatal conductance and transpiration rate thus avoid leaf water loss under drought conditions. Also, comparatively *S. pennellii* exhibits lower stomatal density and aperture. The genes involved in amino acid metabolism and ethylene/Jasmonate pathways are elucidated as key factors in the drought tolerance of *S. pennellii* (Egea et al. 2018). The natural variation that exists for plant water use efficiency (WUE) may be explored as it can contribute to yield under water limited conditions. The carbon isotope composition is being used as measure of plant WUE as both vary in concert in C3 plants. A dominant QTL for carbon isotope composition was detected on chromosome 5 using introgression lines of *S. pennellii*. The markers linked to this QTL can be used in MAS for enhancing WUE in tomato (Xu et al. 2008). The breeding effort to exploit the other wild species for drought tolerance in tomato is limited. With the availability of genetic resources and genomic resources on a pan-genome scale, the efforts are likely to focus more on climate resilience in tomato.

1.7 Brief Account of Molecular Mapping of Tolerance Genes and QTLs

1.7.1 Genomic Studies on Abiotic Stress Tolerance in Tomato

Land plants due to their sessile nature have to endure the harsh environmental conditions. These harsh environmental conditions are collectively labelled as abiotic stresses. Abiotic stresses like high salinity, flood, drought, extreme heat and cold pose a great threat to agriculture (Wang 2003; He et al. 2018). Conventional breeding approach is time consuming, untargeted and hence laborious. Marker assisted breeding and transgenic approaches to obtain elite lines of plants are necessary to meet the ever growing global demands (Ahmar et al. 2020). *Solanum lycopersicum*, commonly known as tomato is sensitive to some abiotic stress like heat and drought but can show tolerance towards moderate levels of salinity (Ayenan et al. 2019; Ors et al. 2021). The breeding of the commercial tomato with the wild species, *Solanum pimpinellifolium* the larger of two genomes (811 Mb), will help immensely as it is a treasure chest for abiotic stress tolerance genes (Razali et al. 2018). Molecular markers can be used to differentiate between multiple varieties aiding in diversity analysis or identify QTLs that impart a specific trait in this case abiotic stress tolerance. In addition to that, transgenic plants can be created to better tolerate the various harsh environmental conditions. The various studies exploring these ideas in tomato related to abiotic stress tolerance are discussed below.

1.7.2 Genomic Diversity Analysis

Molecular and phenotypic evaluations offer an easy way to differentiate between species and the genetic divergence. The molecular evaluation provides deeper insights into the genetic structure whereas the phenotypic counterpart offers less than adequate variations for the intraspecific discrimination and is affected by environmental conditions (EL-Dijkhuizen et al. 1996; Mansy et al. 2021). Molecular markers can be used in diversity analysis with respect to specific characters by subjecting the plants to various stimuli. High temperature stress tolerance is one of the most widely researched topics and rightly so because of the threat of global warming due to climate change. The trends indicate that the average global temperature will rise from 1 °C to 3.7 °C from years 2081–2100 comparing 1986–2005. The increase in temperature will adversely affect tomato production. Even a rise of 1 °C in the average daily temperature can have disastrous impact on the plant's survival (Ayenan et al. 2019).

Six lines of tomato were chosen for the evaluation of heat stress tolerance and diversity between them was established with the help of various molecular markers. A total of 13 unique ISSR, RAPD and SCoT markers were identified in the study (EL-Mansy et al. 2021). Similar study involving 22 tomato accessions from different

parts of India resulted in the identification of 10 SSR markers related to heat stress and three related to more than one trait (Amrutha et al. 2021). A study involving 15 tomato genotypes, including four local varieties of Turkey, 10 heat tolerant varieties obtained from Asian Vegetable Research and Development Center and one *S. pimpinellifolium*, were screened for heat tolerance. The SSR, SRAP markers were employed to identify the differences. Thirty six polymorphic SSR markers with 44.7% polymorphic bands, and 11 SRAP markers with 28 polymorphic bands were reported (Comlekcioglu et al. 2010). Eleven commercial tomato genotypes were analysed under heat stress using 20 RAPD, 15 ISSR markers, individually and together. They yielded, 25, 38 and 31.5 polymorphic bands in combination, respectively (Mansour et al. 2009).

Plants can have similar responses to drought, salinity and sodicity stresses, as it is a common phenomenon in the arid and semi-arid regions of the world. Both can result in the production of ROS which alter the normal cellular metabolism in plants (Dajic 2006; Uddin et al. 2016; Arif et al. 2020). High salinity conditions reduce the ability of plants to absorb water as a result of low water potential around root system. It leads to reduction in growth rate similar to drought stress effects. The combined effects of salinity and drought are more severe on plants than their occurrence individually (Dasgan et al. 2018; Ors et al. 2021). The response to salt and drought stress in plants involves osmotic and ionic signalling to re-establish cellular homeostasis, detoxification to repair the damage caused by stress and signal and co-ordinate cell division to achieve growth (Zhu 2003). Tomatoes are moderately sensitive to salinity but can be affected under severe drought conditions (Ors et al. 2021).

Gharsallah et al. (2016) studied three tomato varieties commonly grown in Tunisia under salt stress and identified 19 polymorphic SSR markers. They also used genotypic and phenotypic associations from multiple loci into a multi-layered network which can guide in the introgression of traits related to salinity stress. SNP markers can be used to identify variations in genes related to specific stress. Ninety four genotypes were subjected to SNP analysis with respect to four genes, *DREB1A*, *VPI1*, *NHX1*, and *TIP*. The researchers identified 5 SNPs/InDels in two of the four genes (*DREB1A*, *VPI1*) accounting for 17 to 25% of phenotypic variation related to salinity tolerance (Rao et al. 2015). Fifteen tomato cultivars were used to observe the diversity with respect to drought stress using ISSR markers by Metwali et al. (2016). Ten ISSR markers were identified with polymorphic ratio percentage ranging from 14.5 to 62.5%. The 15 genotypes showed clear cut genotypic differences and their potential are used in breeding programmes. Molecular markers used in various diversity analysis studies are presented in Table 1.4.

Table 1.4 Different molecular markers used in various diversity analysis related to different abiotic stress in tomato

Stress	Marker type	Number of Unique markers	Number of accessions/genotypes	References
Heat	ISSR, RAPD and SCoT	13	6	EL-Mansy et al. (2021)
	SSR	10	22	Amrutha et al. (2021)
	ISSR and SRAP	47	15	Comlekcioglu et al. (2010)
	ISSR and SRAP	35	11	Mansour et al. (2009)
Salinity	SSR	19	3	Gharsallah et al. (2016)
	SNP	5	94	Rao et al. (2015)
Drought	ISSR	10	15	Metwali et al. (2016)

1.8 Different Markers Used to Identify QTLs Related to Abiotic Stress Tolerance

The response towards abiotic stress at the gene level, can be non-specific as shown by Foolad et al. (2003a) when they discovered QTLs on chromosomes 1 and 4 which was responsible for cold, drought and salinity stress tolerance. However, they discovered stress tolerance specific QTLs as well. The efforts of identifying QTLs related to abiotic stresses in tomatoes are summarized below.

1.8.1 Heat Stress

Several studies have been conducted based on molecular markers to identify QTLs related to heat stress tolerance in tomato. The use of an eight way MAGIC (Multi-Parental Advanced Generation Inter Cross) and a CC (Core Collection) population to identify QTLs related to heat stress was explored by Bineau et al. (2021). The 166 and 98 unique QTLs including 69 pQTLs (plasticity QTLs) related to heat stress tolerance in both the populations were identified. A study where a Recombinant Inbred Line (RIL) of a cross between *S. lycopersicum* cv. Money maker and *S. pimpinellifolium* (accession CGN14498) aided in the investigation of the effects of various environmental stresses with varied nutrient supplements (low nitrogen and high phosphate) and identification of 13 QTLs using a linkage map published in an earlier study (Geshnizjani et al. 2020; Kazmi et al. 2012). In another RIL of the same cross, Gonzalo et al. (2020) using the SNP SOLCAP Infinium chip designed by Sim et al. (2012) reported three newly identified QTLs on chromosomes 2, 3 and 4 in plants grown at higher temperatures (35 °C). It also must be noted that they

reported 20 other QTLs related to fruit trait under heat stress in plants grown at lower temperatures (25 °C and 30 °C).

The use of meta-analysis to identify highly relevant QTLs was performed by Ayenan et al. (2019). They identified 13 mQTLs related to heat stress tolerance from studies published earlier (Grilli et al. 2007; Lin et al. 2010; Xu et al. 2017; Driedonks et al. 2018; Wen et al. 2019). Two SNPs associated with heat tolerance were identified which are linked to three known QTLs in the study by Ruggieri et al. (2019). One of the SNPs (solcap_snp_sl_33830) was present in the gene coding for cytochrome P450 and other the gene is yet to be identified. They also reported few other SNPs that are related to genes imparting high temperature tolerance. A combinatorial approach would result in identification of more relevant QTLs. Such an approach where QTL-Seq analysis and conventional mapping was done by Wen et al. (2019) resulted in the discovery of five consensus heat stress tolerance related QTLs with four candidate genes.

Through genotyping and identifying SNPs, Xu et al. (2017) identified 13 QTLs, one of which was linked to pollen viability in the F2 population of Nagcarlang and NCHS-1 cultivars of tomato. Driedonks et al. (2018) using heat tolerant *S. pimpinellifolium* with either a heat susceptible, *S. lycopersicum* cultivar Moneyberg (MB) or a heat susceptible *S. pimpinellifolium*, identified 13 QTLs related to heat stress tolerance. In another study, RAPD, ISSR and AFLP markers were used to identify 21 QTLs by Lin et al. (2010) where a cross between heat-tolerant breeding line, CL5915-93D4-1-0-3 (*Solanum esculentum*) and a heat-sensitive wild accession, L4422 (*S. pimpinellifolium*) were used. These QTLs were related to fruit characteristics, seed number and Brix value.

Yeh et al. (2006) have used the same markers to identify 6 QTL regions related to various traits linked to heat stress tolerance. Grilli et al. (2007) using Fluorescent Amplified fragment length polymorphism (FAFLP) identified 6 QTLs related to heat stress tolerance in a cross between Jab-95 (heat-tolerant) and cultivar Caribe (heat-susceptible). In a related note, a marker-trait analysis study conducted on 10 tomato genotypes was used to identify SNPs and InDels associated with key heat stress response genes. The genotype, E42 showed 129 polymorphic sequences derived from the stress tolerant wild type *S. pimpinellifolium* (Olivieri et al. 2020). The identified QTLs related to heat stress are presented in Table 1.5.

1.8.2 Salinity Stress and Drought Stress

Various studies have been conducted to understand the molecular mechanisms behind salt and drought stress tolerance and to identify molecular markers that differentiate the superior tolerant varieties in tomato. Grafting conferring tolerance against abiotic stresses is well established (Zijlstra et al. 1994; Schwarz et al. 2010; Colla et al. 2013; Meimandi et al. 2020; Singh et al. 2020). In a study conducted to identify the genetic differences between grafted and the un-grafted RIL of *Solanum pimpinellifolium* lines, Asins et al. (2021) identified 46 QTLs related to water-deficit stress tolerance

Table 1.5 List of identified QTLs and associated traits and chromosomal location related to heat stress tolerance in tomato

No. of QTLs	Marker	Chromosome(s)	Traits	References
69 (pQTLs)	SNP	1–12	Soluble solid content, pH, Number of fruits, Plant height, leaf length, Fruit set, Fruit weight, Fruit colour Stem diameter, Flowering time, No. of flowers	Bineau et al. (2021)
13	SNP	1,4,6, 10 and 11	-	Geshnizjani et al. (2020)
22	SNP	1, 2, 4, 6, and 12	Flower number, Fruit set, Fruit set proportion, Stigma exsertion, Pollen tube germination, Pollen viability	Gonzalo et al. (2020)
13 (mQTLs)	–	1, 2, 3, 9, 11 and 12	Pollen viability, Pollen number, Style protrusion, Anther length, Number of flowers per inflorescence, Inflorescence number, Relative electrical conductivity, Chlorophyll content, Fv/Fm	Ayenan et al. (2019)
5 (consensus QTLs)	SNP	1 and 2	Relative electrical conductivity, Chlorophyll content, F _v /F _m	Wen et al. (2019)
13	SNP	1, 2, 3, 4 7, 9 and 12	Pollen viability, Pollen number, Style protrusion, Style and Anther length	Driedonks et al. (2018)
13	SNP	1, 2, 3, 7, 8 and 11	Pollen viability, Pollen number, Style protrusion, Style and Anther length	Xu et al. (2017)
21	ISSR, RAPD and AFLP	–	Fruit weight, Fruit number, Brix value, Fruit setting, Seed number and Flower number	Lin et al. (2010)
6	ISSR, AFLP and RAPD	2, 3 and 4	Yield	Yeh et al. (2006)
6	FAFLP	–	Fruit set	Grilli et al. (2007)

with candidate genes including transcription factors having significantly enriched GO terms. These include genes involved in cell wall, root development, osmotic and hydraulic adjustments. In 2015, Asins and others identified 7 QTLs relating to transport of four macro and micro nutrients in leaf (K, B, Mg and Mo) and total solid contents in fruit in moderately salt-stressed 130 F₁₀ grafted lines of the hybrid between a salt-sensitive genotype of *Solanum lycopersicum* var. Cerasiforme and a salt-tolerant line from *S. pimpinellifolium*.

Geshnizjani et al. (2020) identified 14 and 27 QTLs related to salt and drought stress tolerance, respectively using SNPs identified earlier by Kazmi et al. (2012). Studies by Diouf et al. (2018, 2020), revealed 46 DEGs (Differentially Expressed Genes) between drought-stressed and control tomato plants associated with 35 QTLs previously identified in eight tomato genotypes related to drought stress. Another study into the effect of drought stress on cultivated tomato identified 11 QTLs of which two were labelled as interactive QTLs with genes related to water deficit stress (Albert et al. 2016). Nineteen drought stress related QTLs were identified on chromosome 9 of the NIL population of cross between *S. habrochaites* and *S. lycopersicum*. Most QTLs were identified on the centromeric end suggesting an area of valuable alleles belonging to the wild type (Lounsbury et al. 2016).

Two introgression lines (IL) of *Solanum pennellii* and *Solanum lycopersicoides* were used to identify six QTLs related to salt stress at seedling stage (Li et al. 2011). Estañ et al. (2009) reported eight QTLs related to fruit yield due to salinity tolerance from the wild type species in the F9 population of the cross between *Solanum lycopersicum* var. *cerasiforme*, as female parent, and two salt tolerant lines, as male parents, from *S. pimpinellifolium* and *S. cheesmaniae*. Villalta et al. (2007) also reported eight QTLs related to salinity tolerance from the F7 population of the same crosses.

Foolad et al. (2003b) identified four QTL regions specific to drought stress tolerance using RFLP markers in crosses between different accessions of *L. esculentum* and *L. pimpinellifolium*. Six QTL regions specific to salt stress using RFLP markers in a cross between *L. esculentum* and *L. pimpinellifolium* were identified and later in the same cross, the effect of salt stress in germination and vegetative stages of tomatoes revealed seven and six QTLs, respectively (Foolad et al. 1998a; 2001; Foolad 1999). The QTLs identified related to salt and drought stress tolerances are presented in Table 1.6.

1.8.3 Cold Stress

Cold stress or low temperature stress is alienated as chilling stress ($<15^{\circ}\text{C}$) and freezing stress ($<0^{\circ}\text{C}$). After drought stress low temperature stress is most harmful to plants. Tropical plants adapt poorly to cold stress but temperate plants can tolerate freezing temperatures (Chinnusamy et al. 2007; Ritonga and Chen 2020). Generation of ROS due to cold stress can have devastating effects on plants (Rezaie et al. 2020). In tomato, cold temperatures slow down the ripening of tomato fruits. This occurs due to the changes in activity of the hormone ethylene and its response factors (Bergevin et al. 1993; Mata et al. 2019). Also, rapid root chilling in tomatoes impedes water movement from root to shoot having similar effects to water deficit stress (Arms et al. 2015).

When the relative germination rate and chilling index was used to identify QTLs in a population raised from the cross between *S. lycopersicum* and *S. pimpinellifolium*, nine QTLs related to cold stress tolerance were identified (Liu et al. 2016). Water

Table 1.6 List of identified QTLs, associated traits and chromosomal location related to salinity and drought stress tolerance in tomato

Type of abiotic stress	No. of QTL	Marker	Chromosome(s)	Traits	References
Drought stress	46	SNP	1–12	Shoot water content, Xylem sap (ABA, Mg, Mn, B, Zr, P)	Asins et al. (2021)
	27	SNP	1, 2, 3, 4, 5, 6, 8, 11 and 12	–	Geshnizjani et al. (2020)
	35	SNP	1–12 (except 5)	Time to flower, Fruit weight, Soluble solid content, Time to ripe, Fruit firmness, Leaf length	Diouf et al. (2018)
	56	SNP	2, 3, 4, 6, 7, 8, 9, 11, 12		Albert et al. (2016)
	19	SNP	9	Days to first green fruit and ripe fruit, Total fruit yield, Shoot dry weight, Ratio of ripe fruit to total yield, Leaf area, Phenolic content	Lounsbury et al. (2016)
	6	RFLP	1, 4, 8, 9 and 12	–	Foolad et al. (2003b)
Salinity stress	14	SNP	4, 5, 6, 7, 8 and 10	–	Geshnizjani et al. (2020)
	7	SNP	1–12	Soluble solid content, Citric acid, Leaf dry weight, Fruit weight, Leaf fresh weight, Macro and micro nutrients	Asins et al. (2015)
	6	RFLP	4, 6, 9 and 12	–	Li et al. (2011)
	8	SSR	3, 5, 6, 9 and 11	Total and ripe fruit weight, Number of days to flowering, Number of fruits,	Estañ et al. (2009)
	8	SSR	1, 3, 5, 6, 7, 11 and 12	Dry leaf and stem weight, Leaf area, Na and K content in stem and leaves, Total Na content	Villalta et al. (2007)
	6	RFLP	1, 2, 5, 7 and 12	–	Foolad et al. (1998a)
	7 and 6	RFLP	1, 2, 3, 5, 7, 6 and 9, 11 and 12	–	Foolad (1999); Foolad et al. (2001)

Table 1.7 List of identified QTLs, associated traits and chromosomal location related to low temperature stress tolerance in tomato

No. of QTLs	Marker	Chromosome(s)	Traits	References
9	SSR	1, 2, 3, 4, 9 and 12	Relative germination rate, Chilling index	Liu et al. (2016)
7	RFLP	1, 5, 6, 7, 11 and 12	2 h cold stress, 6 h recovery post cold stress	Truco et al. (2000)
3–5 putative QTLs	RFLP	1 and 4	–	Foolad et al. (1998b)

deficit due to root chilling has been studied by Arms et al. (2015) and have performed a high resolution mapping of a region in chromosome 9 named *stm9*, initially identified by Truco et al. (2000) with 22 putative genes. Truco et al. (2000) have also identified several QTLs related to chilling stress using RFLP markers. After two hours under cold stress, three QTLs were responsible for wilting with a QTL on chromosome 6 having a negative effect. In the recovery after six hours, it is reported that four QTLs were responsible. The MAPMAKER/QTL and QGENE software were used to identify 3–5 cold stress related QTLs in a cross between cold sensitive *L. esculentum* and *L. pimpinellifolium* (Foolad et al. 1998b). In tomato many QTLs related to a specific stress tolerance are identified and this makes understanding the performance of tomato under harsh environmental conditions much easier. The QTLs related to low temperature stress are listed in Table 1.7.

1.9 Genes Orchestrating Abiotic Stress Tolerance in Tomato and Transgenic Efforts

Discovering the genomic regions that are involved in abiotic stress tolerance is necessary to develop and select lines that are better at withstanding harsh environmental conditions. Understanding the regions imparting stress tolerance requires the identification of the genes pulling the strings. The key genes imparting abiotic stress tolerance code for regulatory proteins like transcription factors, functional proteins and other proteins for the protection of biomolecules that are necessary for the survival of the cell and plant as a whole (Agarwal et al. 2006). Studies on the transcriptome of plants under stress reveals key genes by highlighting the DEGs that play a role in various abiotic stress tolerance (Weiss and Egea-Cortines 2009; Bitá et al. 2011; Chen et al. 2015a, b; Cruz-Mendivil et al. 2015; Fragkostefanakis et al. 2016; Liu et al. 2017; Zhang et al. 2017b; Bouzroud et al. 2018; Mu et al. 2021b).

Transcription factor families like MYB, AP2/ERF, NAC, WRKY, bZIP have been reported to regulate abiotic stress response in tomato (Yáñez et al. 2009; Hsieh et al. 2010; Sharma et al. 2010; Cao et al. 2013; Zhu et al. 2014; Hichiri et al. 2017; Klay et al. 2018; Gao et al. 2020; Zhu et al. 2020). Since, transcription factors regulate

gene expression, understanding their roles and the genes they regulate is necessary. The MAPK pathway gets triggered under abiotic stress. Genes like *SIMP1*, 2 and 3 are involved in response to heat and oxidative stress (Nie et al. 2012; Li et al. 2014). Calcium mediated signaling is carried out by calcium binding proteins which, in turn binds to the specific CAMTA transcription factor in the family. In case of elevated salt levels in the environment, the SOS salt response pathway comes in to effect. One of the proteins SOS3 (calcium binding protein), senses the calcium levels in the cell and activates SOS2 (Serine /Threonine kinase) and through SOS1 (Na^+/H^+ transporter) the excess salt is transported out of the cell (Ishitani et al. 2000; Huertas et al. 2012; Noman et al. 2021). Production of ROS is necessary under abiotic stress since it plays role along with hormones and other signaling mechanisms in responding to stress (Devireddy et al. 2021). The ROS formed under various stresses has to be scavenged since it can have harmful effects on the cell. Enzymes like SOD, CAT, ascorbate peroxidase (*APX*), dehydro ascorbate reductase (*DHAR*), glutathione reductase (*GR*), mono dehydro ascorbate reductase (*MDHAR*) and guaiacol peroxidase (*GPX*) help in scavenging the formed ROS before it causes irreversible damage (Das and Roychoudhury 2014). A transcription factor *SIGRAS10* when down regulated resulted in elevated levels of the scavenging enzymes and ultimately reduced the levels of ROS (Krishna et al. 2019; Habib et al. 2021). Recent efforts on transgenic approach towards tolerance towards abiotic stress are highlighted in Table 1.8.

Once the roles of genes are understood, the logical next step is to check the effects of overexpressing or silencing said genes. It can also be used to understand the function of the gene as well. Apart from that, expression or overexpression of foreign proteins that have superior properties to their native counterparts have been attempted. These studies give us insights in to the various genes that can be used to impart a specific stress tolerance.

1.10 Sol Genomics

It is used to store genetic and genomic information, for Solanaceae species, such as tomato, potato, tobacco, pepper, eggplant and petunia. It is a community driven, genome sequence based database where users can update and delete sequence related information. It functions as a model organism database (MOD) but it is community curated (Fernandez-Pozo et al. 2015). The sequencing of a high quality reference resulted in mapping sequences of other genomes on to the corner stone sequence (Mueller et al. 2005). It has various tools related to sequencing, mapping and two tomato specific tools i.e., Tomato Expression Atlas and Tomato Expression Database. It contains information on the various wild type species related to tomato and that can be helpful for introgression of abiotic stress traits into the commercial varieties. The genes that are annotated, including the abiotic stress related genes can be helpful in analysing one's transcriptome data.

SolCyc, a set of Pathway/Genome Databases (PGDB) provide information on the metabolic pathways and enzymatic reactions for the Solanaceae species. The Sol

Table 1.8 List of transgenes and effects related to different abiotic stress tolerance

Type of stress	Modification	Effects	References
Drought stress	Overexpression of <i>SINAC6</i>	Delay in growth; reduced water loss and oxidative damage	Jian et al. (2021)
	Co-overexpression of <i>AtDREB1A</i> and <i>BcZAT12</i>	Enhanced drought tolerance; reduced electrolyte leakage, H ₂ O ₂ and elevated level of relative water content, chlorophyll colour index	Krishna et al. (2021)
	Overexpression of <i>SIGATA17</i>	Better drought tolerance through regulating the activity of the PAL gene of the phenyl propanoid pathway	Zhao et al. (2021)
	Overexpression of <i>SIGRAS4</i>	Enhanced drought stress tolerance and upregulation of genes for ROS scavenging enzymes due to interaction with positive regulators of ABA signalling	Liu et al. (2021)
	Silencing of <i>SLB3</i>	Decreased drought tolerance and decreased levels of SOD enzyme, increased ROS, proline and peroxidase enzyme	Wang et al. (2020c)
	Crispr cas9 mediated <i>SIMAPK3</i> knockout	more severe wilting symptom, higher hydrogen peroxide content, lower antioxidant enzymes activities, and suffered more membrane damage under drought stress. Up- or down-regulated expressions of drought stress-responsive genes including <i>SILOX</i> , <i>SIGST</i> , and <i>SIDREB</i>	Wang et al. (2017)
Salinity stress	Overexpression of sly-miR398b	Decreased plant growth and reduced biomass; downregulation of scavenging enzymes and consequent increase in O ₂ radicals	He et al. (2021)
	Overexpression of <i>SIBZR1</i>	Reduced plant growth, delayed flowering, smaller and curly leaves; upregulation of stress related genes	Jia et al. (2021)
	Overexpression of <i>LeNHX4</i>	Increased fruit number and size under salinity and normal conditions; increased tolerance to salinity stress	Maach et al. (2020)
	Co-overexpression of <i>LeNHX2</i> and <i>SISOS2</i>	Increased tolerance to salinity, increased yield, biomass, proline levels and total soluble solids in fruit	Maach et al. (2021)
	Overexpression of <i>SICOMT1</i>	Improved salt stress tolerance by altering melatonin levels, higher levels anti-oxidant enzyme activity and higher ascorbic acid (AsA) and glutamate (GSH) accumulation levels	Sun et al. (2020)
	Crispr Cas9 mediated partial excision of <i>SIHyPRP1</i>	Various excised motifs of the <i>SIHyPRP1</i> exhibited varied results with respect to growth and germination with most being better than the WT	Tran et al. (2021)

(continued)

Table 1.8 (continued)

Type of stress	Modification	Effects	References
Heat stress	Overexpression of <i>HsfB1</i>	Overexpression leads to the accumulation of phenols, flavonoids due to upregulation of genes involved and knock down leads to accumulation of polyamine putrescine, glucose and sucrose	Paupière et al. (2020)
	Overexpression of <i>SIWHY1</i>	Upregulation of <i>SIHSP21.5A</i> leading to increased membrane stability, soluble sugar content and reduced ROS contributing to heat tolerance	Zhuang et al. (2020)
	Overexpression of <i>SISNAT</i>	Increased levels of melatonin and thermotolerance and interaction with HSP40 protect the SNAT enzyme	Wang et al. (2020b)
Cold stress	Overexpression of <i>SiFBA5</i> (<i>Saussurea involucrata</i>)	Increased cold tolerance, malondialdehyde, CAT, SOD and POD production and improved photosynthetic efficiency due to increased FBA expression in chloroplasts and promoted Rubisco expression	Mu et al. (2021a)
	Overexpression of <i>BoCRP1</i> (<i>Brassica oleracea</i>)	Increased tolerance to chilling stress; overall improved rate of seed germination, increased accumulation of osmoprotectants and increased root length; reduced membrane damage	Wani et al. (2021)
	Overexpression of <i>SIHY5</i>	Better cold tolerance; upregulation of genes related to antioxidant enzymes like SOD and CAT, anthocyanin biosynthesis genes <i>CHS</i> , <i>CHI</i> , and <i>F3H</i> and cold induced genes <i>PRI</i> , <i>CYSb</i> , <i>LEA</i> , <i>Osmotin</i> , and <i>ICE1</i>	Han et al. (2020)

genomics website has a genomic selection tool that relates the genotype and phenotype data to predict the phenotype from genotypic data. Apart from the genotype related data and tools, it offers phenotype database as well (Fernandez-Pozo et al. 2015).

1.11 Conclusion

Tomato being nutritionally an important crop is grown worldwide in diverse geographical regions. Though, better crop management practices and cultivars are available for realizing higher yield, tomato crop is affected by various abiotic stresses during various phenophases. Under climate change conditions the occurrence of these abiotic stresses are likely to increase and cause damage to the production, productivity and quality. In the coming years due to demand from the growing population,

there is a need to enhance the production and sustain productivity and quality. The abiotic stresses may occur either individually or in combination causing adverse effects on the crop. Tomato is sensitive to high temperature, salinity, cold, deficit, and excess moisture stress conditions. Hence, better understanding with respect to molecular, physiological, biochemical and morphological changes occurring due to impact of various abiotic stresses is essential. The literature is replete with information on influence of abiotic stresses at different organizational level of tomato plant. Good information is available on tolerant sources both from cultivated and wild species. However, their exploitation in developing tolerant cultivars employing breeding methods is very limited.

The modern molecular tools employed in identification of QTLs, MAS, genome editing, gene discovery, transgenic approaches have facilitated better understanding of the response of tomato and its wild species with respect to various abiotic stresses. In terms of crop improvement there is reasonable understanding about various sources and traits imparting salinity stress, drought, flooding and other abiotic stresses. We have reasonable knowledge on root traits imparting tolerance to heat, drought, salinity and cold stresses. Knowledge of genomic diversity, genes involved and QTLs associated traits and chromosome location with respect to drought, heat, salinity and cold stresses are being generated and would be used in improvement programmes.

The approach of mining various genotypes with superior qualities for abiotic stress tolerance as well as differentiate them, using ideal, rapid and accurate techniques. The identified QTLs and markers, will aid in breeding programs aimed at producing abiotic stress tolerant lines of tomato. RNA Seq analysis and production of transgenic lines with foreign gene and/or overexpressing or silencing of native genes will help in gaining insights about the genes involved in abiotic stress tolerance. Recently genome editing technology has improved our ability to manipulate the tomato genome. The Sol genomics database is the latest tool with its ease of use and relevant information available for researchers', disposal to further the innovations and improvement of abiotic stress tolerance in tomato.

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