CHAPTER 27

CURRENT STATUS OF BREEDING TOMATOES FOR SALT AND DROUGHT TOLERANCE

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Abstract: Salinity and drought are among the most challenging environmental constraints to crop productivity worldwide. The cultivated tomato, *Lycopersicon esculentum* Mill., is moderately sensitive to both of these stresses throughout its ontogeny, including during seed germination, seedling emergence, vegetative growth and reproduction. Limited variation exists within the cultivated tomato for abiotic stress tolerance, however, the related wild species of tomato is a rich source of genetic variation which can be used for crop improvement. During the past several decades this variation has been utilized for characterization of physiological and genetic bases of tolerance to different abiotic stresses, including salinity and drought. Abiotic stress tolerance is a complex phenomenon, controlled by more than one gene and influenced by uncontrollable environmental factors. Furthermore, tomato stress tolerance is a developmentally-regulated state-specific phenomenon, such that tolerance at one stage of plant development is independent of tolerance at other stages. This has been demonstrated by analysis of response and correlated response to selection as well as identification of quantitative trait loci (QTLs) conferring tolerance at different stages. Transgenic approaches also have been employed to gain a better understanding of the genetic and physiological bases of salt and, to a lesser degree, drought tolerance in tomato, and to develop transgenic plants with improved stress tolerance. However, despite considerable traditional genetics and physiological research as well as contemporary molecular marker and transgenic studies in tomato, there is yet no report of any commercial cultivar of tomato with salt or drought tolerance. To achieve this goal, cooperation among plant geneticists, physiologists, molecular biologists and breeders engaged in tomato stress tolerance is imperative. In this chapter, I review the recent progresses in genetics and breeding of salt and drought tolerance in tomato and discuss the prospects for developing commercial cultivars with stress tolerance

Keywords: breeding, drought stress, drought tolerance, gene mapping, genetic engineering, genetic transformation, quantitative trait loci (QTL), salt stress, salt tolerance, transgenic plants

Abbreviations: BC: backcross; DS: drought stress; DT: drought tolerance; DW: dry weight; FW: fresh weight; h^2: heritability; MAS: marker-assisted selection; PS: phenotypic selection; QTL: quantitative trait loci; RIL: recombinant inbred line; SG: seed germination; SS: salt stress; ST: salt tolerance; TI: tolerance index; VS: vegetative stage; WUE: water use efficiency

1.   INTRODUCTION

1.1.   The Tomato

The cultivated tomato, *Lycopersicon esculentum* Mill., is the 2nd most important vegetable crop in the world in terms of consumption per capita and is the most popular garden vegetable. In addition to tomatoes that are eaten directly as raw vegetable or added as ingredient to other food items, a variety of processed products have gained popularity. Although a tropical plant, tomato is grown in almost every corner of the planet. It is grown in greenhouses where summers are too cool for pollination or fruit set to occur in outdoors. Worldwide, a total of 4,528,519 ha of tomato were harvested in 2005 with a total production of 124,748,292 Mt (FAOSTAT 2005). Major production countries in descending orders include China, U.S.A., Russia, Turkey, India and Italy. In the U.S., it is the 3rd most economically important vegetable crop (with a total farm value of $2.062 B) after potato ($2.564 B) and lettuce ($2.064 B) (http://www.usda.gov/nass/pubs/agr05/agstats2005.pdf). In the U.S., total harvested area in 2004 was 170,808 ha (505,60 ha fresh-market tomatoes valued $1.34 B and 120,248 ha processing tomatoes valued $0.72 B) (http://www.nass.usda.gov:8080/QuickStats/index2.jsp). California is by far the leading producer of processing tomatoes followed by Florida, which is also the leading state in producing fresh tomatoes (USDA 2005). Per capita consumption in the U.S. includes 31.7 kg of processing and 8.7 kg of fresh tomatoes (http://www.ars.usda.gov/). Although tomatoes do not rank high in nutritional value, they contribute significantly to the dietary intake of vitamins A and C and essential mineral and nutrients. In the U.S. diet, tomato ranks first among all fruits and vegetables as a source of vitamins and minerals (Rick 1980). Also, tomatoes are the richest source of lycopene, a phytochemical that protects cells from oxidants that have been linked to cancer (Giovannucci 1999).

Tomato belongs to the nightshade family *Solanaceae*, which is the most variable of all crop families in terms of agricultural utility, the third most economically-important after grasses and legumes, and the most valuable in terms of vegetable crops. The genus *Lycopersicon* is one of the smallest genera in *Solanaceae*, though the centerpiece for genetic and molecular research in the family. There are 9 known species within *Lycopersicon*, including the cultivated type *L. esculentum* and its wild form *L. esculentum* var. *cerasiforme* (Dun.) Gray, and the 8 wild species *L. pimpinellifolium* (Jusl.) Mill., *L. cheesmanii* Riley, *L. chmielewskii* Rick, Kes., Fob. & Holle, *L. chilense* Dun., *L. parviflorum* Rick, Kes., Fob. & Holle, *L. peruvianum* (L.) Mill., *L. hirsutum* Humb. and Bonpl. and *L. pennellii* (Corr.) D'Arcy (Rick 1976a; Rick 1979b). All species are native to western S. America, between Ecuador and Chile (Rick 1976b). However, their natural habitat is variable, from very dry to very wet, and from coastal to mountainous areas of more than 3300 m elevations (Warnock 1988). Among the 9 species, only *L. esculentum* has become a domesticated crop (Rick 1978), which includes the common fresh-market and processing tomatoes, land races, primitive cultivars, and the wild cherry, *L. esculentum* var. *cerasiforme*.

All tomato species are diploid (2N = 2X = 24) and have the same chromosome number and structure. Tomato is one of the most genetically characterized higher plant species and an excellent model system for basic and applied research. This is due to many reasons, including ease of culture, short life cycle, high self-fertility and homozygosity, great reproductive potential, ease of use for controlled pollination and hybridization, availability of a wide array of mutants and genetic stocks (http://tgrc.ucdavis.edu/; http://www.sgn.cornell.edu/), diploid with a rather small genome (0.86 pg, 950 kb) (Arumuganathan and Earle 1991), and amenability to asexual propagation and protoplast, cell and tissue cultures and whole plant regeneration thereof (McCormick et al. 1986). Members of *Lycopersicon* are easily transformed and transgenic tomatoes are routinely produced using *Agrobacterium tumefaciens* (McCormick et al. 1986). Recent availability of high MW insert genomic libraries of tomato has facilitated map-based gene cloning, and advances in EST databases and genome sequencing have added additional tools for further expansion of basic and applied research in tomato.

1.2. Sources of Genetic Variation and Response to Environmental Stresses

The cultivated tomato has a narrow germplasm base, largely because of several genetic bottlenecks that occurred during domestication and evolution of modern cultivars (Rick 1976b). Although higher levels of variability can be found in primitive cultivars in the native regions of tomato, it is estimated that only about 5% of the total genetic variation within *Lycopersicon* is within the cultivated species (Miller and Tanksley 1990; Rick and Fobes 1975). As a consequence, genes for many desirable agricultural characteristics, including environmental stress tolerance, are not found within *L. esculentum*. Fortunately, however, the related wild species of tomato are a rich source of desirable genes and characteristics for tomato crop improvement, all of which can be hybridized with the cultivated species, though with different degrees of difficulty (Rick 1976a, 1979a; Rick et al. 1987). The species with the greatest genetic variability are *L. chilense*, *L. hirsutum*, *L. peruvianum* and *L. pennellii* whereas the least variable species are *L. cheesmanii* and *L. pimpinellifolium* (Breto et al. 1993; Miller and Tanksley 1990). During the past several decades, tomato wild species have been extensively utilized for tomato crop improvement, in particular for improving disease resistance. Comparatively, however, only a superficial assessment of the extent of the genetic variation for environmental stress tolerance within *Lycopersicon* has been made. Nonetheless, some accessions with tolerance to abiotic stresses have been identified and used for characterization of physiological and genetic bases of stress tolerance as well as for improving crop stress tolerance. In this chapter, the existing variation in *Lycopersicon* in relation to salt and drought tolerance and the recent advancements in genetics and breeding of stress tolerance are reviewed and discussed.

1.3.   Production Environments

Tomato is grown under wide varieties of climates ranging from tropics to within a few degrees of the Artic Circle. However, despite its global distribution, a major portion of the world tomato production is concentrated in a number of warm and dry regions, in particular areas around the Mediterranean Sea, southern and western parts of the U.S., and Mexico. These climates on the other hand are prone to drought and/or salinity stress during tomato production. For various reasons, nearly all tomato-breeding programs have largely focused their breeding activities on developing cultivars with high yield potential under favorable (i.e., nonstress) conditions. This is similar to the situation in many other crop species, where such breeding efforts have resulted in improved efficiency of crop production per unit area (Duvick 1986). In case of processing tomato, for example, the average-yield per unit area in the U.S.A. increased by seven fold between 1920s and 1990s (Warren 1998). However, with the rapid increase in human population and a greater demand for food, and with an increasing diminution in natural resources and arable lands, greater efforts must be devoted to increasing crop productivity in stressful agricultural environments as well as bringing marginal lands under cultivation. Although soil reclamation and deliberate irrigation management could alleviate stresses due to salinity or drought, development of cultivars with stress tolerance is considered a complementary approach to achieve higher yields in stressful environments. This approach has been suggested as an effective and economic solution to crop production in stress environments (Blum 1988). Toward this goal, within the past few decade considerable research has been undertaken and significant information has been obtained regarding the physiology, genetics and breeding of tomatoes for stress tolerance. In this chapter, the current information on tomato response to salt and drought stress and the available genetic resources for stress tolerance breeding are reviewed and the prospects for developing commercially acceptable, stress-tolerant tomato cultivars through conventional breeding and genomic approaches are discussed. In the following sections, each of the two stresses is dealt with separately.

2.   GENETICS OF AND BREEDING FOR SALT TOLERANCE IN TOMATO

2.1.   Background

Commercial cultivars of tomato are moderately sensitive to salinity at all stages of development, including seed germination, vegetative growth, and reproduction (Jones et al. 1988; Maas 1986). Genetic resources for salt tolerance (ST), however, have been identified within tomato related wild species. Attempts to find sources of genes for ST in tomato were first made by Lyon (Lyon 1941), who suggested that ST of the cultivated tomato might be improved by introgression of genes from *L. pimpinellifolium*, the most closely related wild species of tomato. Later investigations resulted in identification of other salt-tolerant accessions within this

and other wild species, including *L. peruvianum* , *L. cheesmanii* , *L. hirsutum* and *L. pennellii* (Foolad and Lin 1997b; Jones 1986a; Phills et al. 1979; Rush and Epstein 1976; Sarg et al. 1993; Tal 1971; Tal and Shannon 1983). However, it is expected that more salt-tolerant accessions can be found within the wild species of tomato if more comprehensive screenings were conducted (Foolad 2004; Foolad and Lin 1997b).

In tomato (Asins et al. 1993a; Foolad 1999; Foolad and Lin 1997a; Jones and Qualset 1984) as well as many other plant species (Ashraf and McNeilly 1988; Johnson et al. 1992; Mano and Takeda 1997; Quesada et al. 2002) ST at each stage of plant development is often independent of tolerance at other stages. Also, in general ST of a plant is increased with its age in many species, including tomato (Bolarin et al. 1993), barley (*Hordeum* spp.), corn (*Zea mays* L.), rice (*Oryza sativa* L.) and wheat (*Triticum* spp.) (Maas 1986). Therefore, to facilitate a better understanding of the genetics of ST, in tomato often individual developmental stages have been studied for assessment of tolerance and the identification, characterization and utilization of useful genetic components. Below, recent findings on genetics of ST in tomato during different developmental stages are briefly reviewed and discussed.

2.2. Salt Tolerance During Seed Germination

Commercial cultivars of tomato are most vulnerable to salt stress (SS) during seed germination (SG) and early seedling growth stages (Cook 1979; Foolad and Jones 1991; Foolad and Lin 1997b; Jones 1986b; Maas 1986), when they exhibit sensitivity even to low concentrations (∼75 mM) of salt (Cuartero and Fernandez-Munoz 1999; Foolad and Lin 1997b; Jones 1986a). Surface soils, however, may have salinities several fold that of the subsoil, presenting a serious problem during SG and seedling emergence. High salinity delays the onset, reduces the rate and final percentage of germination, and increases the dispersion of SG events in tomato. This sensitivity has important biological and applied significance. The costly operations of greenhouse seedling production and transplantation into the field are good reasons for tomato producers to consider growing direct-seeded crops. However, the dependence upon mechanization in modern cultivation systems and the use of costly hybrid seed, requires rapid, uniform and complete SG. Genetic resources for ST during SG have been identified within primitive cultivars and related wild species of tomato, including *L. pennellii*, *L. pimpinellifolium* , and *L. peruvianum* (Cuartero and Fernandez-Munoz 1999; Foolad and Lin 1997b; Jones 1986a). Salt-tolerant accessions have been utilized for investigation of the physiology and genetics of ST during SG in tomato.

2.2.1. *Physiology of seed germination under salt stress*

Salt tolerance during SG is a measure of the seed's ability to withstand the effects of salts in the medium. Excessive salt depresses the external water potential, making water less available to the seed. Slower SG under SS compared to nonstress

conditions, however, could be due to osmotic and/or ionic effects of the saline germination medium. Physiological investigations to distinguish between the two types of effects have been scarce. However, accumulating evidence in different crop species suggests that low water potential of the external medium, rather than ion toxicity effects, is the major limiting factor to germination under SS (Bliss et al. 1986; Bradford 1995; Haigh and Barlow 1987; Kaufman 1969; Ungar 1978), although a few reports have indicated otherwise (Choudhuri 1968; Redmann 1974; Younis and Hatata 1971). In a recent investigation, germination responses of eight tomato genotypes were evaluated in iso-osmotic (water potential ≈ -700 kPa or ≈ 15 dSm^{-1}) medium of NaCl, MgCl$_2$, KCl, CaCl$_2$, sorbitol, sucrose, or mannitol (JR Hyman and MR Foolad, unpubl. data). Comparison of germination in SS treatments with those in osmotic-stress treatments indicated that all genotypes responded similarly to these two types of stresses. Also, comparison of germination among the SS treatments indicated that different types of salt generally affected germination of all genotypes similarly. The results supported the suggestion that the delay in germination of tomato seed under SS was mainly due to osmotic rather than ion-toxicity effects.

2.2.2.   *Inheritance of salt tolerance during seed germination*

Most studies which examined the inheritance of ST during SG in tomato concluded that the heritability (h^2) for this trait was in the range of medium to high and the trait could be improved by directional phenotypic selection (PS). For example, generation means analysis of parental, filial and backcross (BC) populations of a cross between a salt-sensitive breeding line and a salt-tolerant *L. esculentum* plant introduction (PI174263) indicated that the ability of tomato seed to germinate rapidly under SS was genetically controlled with a narrow-sense h^2 of 0.75 ± 0.03 (Foolad and Jones 1991). This conclusion was confirmed in a subsequent study using F_2:F_3 and F_3:F_4 regression analysis of the progeny of the same cross (Foolad and Jones 1992). In a later study, the effectiveness of PS in improving tomato SG under SS was demonstrated using F_2, F_3 and F_4 progeny (Foolad 1996b). This study indicated that directional PS for rapid SG under SS significantly improved progeny ST, indicating a realized h^2 of 0.67–0.76. The overall conclusion from these studies was that ST during SG in tomato was controlled by a few major genes with largely additive effects. However, to verify this and to facilitate marker-assisted breeding of this trait a few genetic mapping studies were pursued, as discussed in below.

2.2.3.   *QTL analysis of salt tolerance during seed germination*

Studies to identify quantitative trait loci (QTLs) for ST during SG in tomato have generally employed interspecific crosses, where presence of molecular marker polymorphisms allowed such studies. In one study, a trait-based marker analysis (a.k.a. selective genotyping) of an F_2 population of a cross between a salt-sensitive tomato breeding line and a salt-tolerant accession (LA716) of *L. pennellii* resulted in the identification of five QTLs on chromosomes 1, 3, 7, 8 and 12 (Foolad and Jones 1993). The validity of these QTLs was examined in a few subsequent studies, using populations derived from the same or different interspecific crosses, including

BC$_1$, BC$_1$S$_1$ and recombinant inbred line (RIL) populations of crosses between *L. esculentum* and *L. pimpinellifolium* (Foolad and Chen 1998; Foolad et al. 1998; Foolad et al. 1997; M.R. Foolad et al., unpubl. data). These studies validated the previously-identified QTLs and detected a few additional QTLs on chromosomes 2 and 9. The combined results supported the notion that ST during SG in tomato was a quantitative trait controlled by more than one gene. Notably, however, in all of these studies it was determined that this trait was controlled by a few QTLs with major effects in addition to several QTLs with smaller effects. A comparison of QTLs indicated that some QTLs were stable across populations/generations whereas others were population-specific. Further comparisons of QTLs across interspecific populations, including those derived from *L. esculentum* × *L. pennellii* (Foolad and Chen 1998; Foolad et al. 1997) and *L. esculentum* × *L. pimpinellifolium* crosses (Foolad et al. 1998; M.R. Foolad, unpubl. data), indicated that some QTLs were conserved across species whereas others were species-specific. Most studies also suggested absence of significant epistatic interactions among QTLs. The overall results from these studies indicate that, in comparison to ST at later stages of development (described in below), ST during SG in tomato is less affected by variation in genetic and environmental backgrounds and thus, it should be feasible to transfer this trait to commercial cultivars by PS or marker-assisted selection (MAS). However, because in most cases tolerance QTLs are found within the wild species of tomato and often more than one gene resource is utilized during the life of a breeding project, the use of MAS may be beneficial.

2.2.4. Comparison of salt tolerance at different stress levels during seed germination

A successful cultivar would be one which exhibits ST at a wide range of SS levels and whose performance would not decline in the absence of salts. This is because in many saline soils the concentration of salts varies across the soil horizon, ranging from low to moderate and high (Richards and Dennett 1980). Practically, however, in a breeding program it may not be feasible to conduct selections under different SS levels. It is, therefore, important to determine whether there is a critical salt concentration at which selections could be made to develop cultivars with ST at most other SS levels. Several studies have been conducted to examine relationships among germination responses under different SS levels in tomato. Evaluation of 56 tomato genotypes for ST during SG at 75 mM (low), 150 mM (intermediate) and 200 mM (high) salt indicated that generally genotypes that germinated rapidly at the low SS level also germinated rapidly at the moderate and high concentrations (Foolad and Lin 1997b). Linear correlation analysis indicated the presence of a strong phenotypic correlation ($r = 0.90$, $P < 0.01$) between germination response at 75 mM and 150 mM salts. The results suggested that the same genes might control the rate of tomato SG under different SS levels. This suggestion was subsequently confirmed by an analysis of response and correlated response to selection for ST, where selections were made separately under low (100 mM), medium (150 mM) or high (200 mM) salt concentration and progeny responses were examined at all three levels (Foolad 1996b). The results indicated that selection for rapid SG at

any SS level led to progeny with enhanced germination rate at all three SS levels, suggesting that similar or identical genes with additive effects were responsible for rapid SG response at different SS levels. This suggestion was consistent with the finding of similar QTLs for ST during SG at different SS levels (Foolad and Jones 1993). The combined results suggest that to develop tomato cultivars with improved ST during SG, it is sufficient to conduct selections at a single SS level, preferably at a medium SS level (Foolad 1996b).

2.2.5.   *Physiological genetics of salt tolerance during seed germination*

Although QTLs for ST during SG in tomato have been identified, their genetic nature or the physiological mechanisms that they modulate have not been determined. However, based on the current knowledge of the physiology of ST during SG, some speculations can be made as to their roles. The tomato seed is comprised of a seed coat that encloses the embryo and an endosperm that practically fills the lumen of the seed not occupied by the embryo (Esau 1953). For germination to occur, the hydraulic extension force of the embryo must exceed the opposing force of the seed coat and the living endosperm tissues (Bradford 1986; Groot and Karssen 1987; Hegarty 1978; Liptay and Schopfer 1983). Embryo genotype was suggested to play a major role in determining the time to germination of tomato seed under nonstress or stress conditions (Liptay and Schopfer 1983). According to this hypothesis, differences in salt sensitivity of tomato seeds during germination reside either in the osmotic potential or pressure potential of the germinating embryo. However, osmotic stress can also negatively affect seed imbibition, and thus retard (or prevent) weakening of the restrictive forces of the endosperm and seed coat, resulting in reduced rate (or inhibition) of germination (Dahal et al. 1990; Groot and Karssen 1987; Liptay and Schopfer 1983). Thus, the rate of SG may be influenced by the physical, chemical, and thus, genetic composition of the embryo, endosperm and/or the seed coat. The identified QTLs for ST during SG in tomato could therefore affect germination rate by affecting the vigor of the germinating embryo, the variation in the thickness of the endosperm, the physical and permeability properties of the endosperm cell walls, the time of onset or rate of activity of enzymes which modify the properties of the endosperm cell wall, the release of gibberellin by the embryo, the base water potential required for SG, the hydrotime constant (Bradford 1995), the rate of metabolic activities in the embryo or endosperm under osmotic stress, osmoregulation during germination, or any other physiological or metabolic processes which are essential for the initiation of germination. However, isolation, characterization and comparison of functional genes which facilitate rapid SG under SS would be necessary to determine the actual roles of the identified QTLs.

2.3.   **Salt Tolerance During Vegetative Stage**

For tomato production under saline conditions, ST during vegetative stage (VS) is more important than ST during SG because most tomato crops are established by seedling transplantation. ST during VS may also be more important than ST

during reproduction (flowering and fruit set) as tomato ST generally increases with plant age and plants are usually most tolerant at maturation (Bolarin et al. 1993). During flowering and fruiting stages, for example, tomato plants can withstand salt concentrations that can kill them at the seedling stage. Most commercial cultivars of tomato are moderately sensitive to SS during VS (Foolad and Lin 1997b; Maas 1986; Tal and Shannon 1983). At low concentrations of salt (EC = 3–5 dSm^{-1}), tomato growth is mainly restricted by nutritional imbalances, as nutrients become the limiting factor under such conditions (Cuartero and Fernandez-Munoz 1999). At moderate to high levels of salt (EC $\geq$ 6 dSm^{-1}), in addition to nutrient imbalances, osmotic effects and ion toxicity contribute to reductions in growth. Phenotypic variation for ST during VS has been identified within the cultivated (Cuartero et al. 1992; Foolad 1997; Sarg et al. 1993) and wild species of tomato, including *L. peruvianum* (Tal and Gavish 1973), *L. pennellii* (Cano et al. 1998; Dehan and Tal 1978; Perez-Alfocea et al. 1994; Saranga et al. 1991), *L. cheesmanii* (Asins et al. 1993a; Rush and Epstein 1976), and *L. pimpinellifolium* (Asins et al. 1993a; Bolarin et al. 1991; Cuartero et al. 1992; Foolad and Chen 1999). This variation has been utilized for investigation of the physiology and genetic basis of ST during VS in tomato.

2.3.1.   *Physiology of salt tolerance during vegetative stage*

Most salt-tolerant genotypes within the cultivated tomato and closely-related wild species *L. pimpinellifolium* generally exhibit a glycophytic response to salinity, that is, exclusion of toxic ions (e.g. Na$^+$) at the root or shoot level and synthesis and accumulation of compatible organic compounds (e.g., sugars and amino acids) for osmoregulation (Bolarin et al. 1993; Caro et al. 1991; Cuartero et al. 1992; Foolad 1997; Perez-Alfocea et al. 1993b; Santa-Cruz et al. 1998). In contrast, salt-tolerant accessions within the tomato wild species *L. pennellii*, *L. cheesmanii* and *L. peruvianum* generally exhibit a halophytic response to salinity, in which osmotic adjustment is achieved by uptake of inorganic ions from the soil and compartmentalization in cell vacuoles (Bolarin et al. 1991; Perez-Alfocea et al. 1994; Sacher et al. 1983; Tal and Shannon 1983). However, differential accumulation of ions has not always been identified as a major factor in determining tomato ST or sensitivity. For example, analysis of BC populations of a cross between a salt-sensitive cultivar and a salt-tolerant *L. pennellii* accession (LA716) indicated that tissue ion content was not likely to provide an efficient selection criterion for ST, as no direct relationship was observed (Saranga et al. 1992). In another study, analysis of the relationship between ST and leaf ion compositions in the cultivated and three wild species of tomato prompted Saranga et al. (1993) to conclude that dry matter production under SS was positively correlated with K$^+$/Na$^+$ ratio in the stem and negatively correlated with Cl$^-$ concentration in leaves and stems. The authors suggested that tissue ion content and ion selectivity were good selection criteria for ST breeding in tomato. Potassium selectivity over Na$^+$ was also reported as a good indicator of ST in a study of several genotypes of the cultivated and wild species of tomato (Cuartero et al. 1992). Further studies of wild species of tomato,

including *L. peruvianum* (Tal 1971), *L. cheesmanii* (Rush and Epstein 1981b) and *L. pimpinellifolium*, *L. hirsutum* and *L. pennellii* (Bolarin et al. 1991), related elevated concentrations of Na^+ in the leaf to plant ST. Other studies suggested that the ability to regulate Na^+ concentration in the leaf tissue was more closely correlated with ST than Na^+ concentration per se (Sacher et al. 1983) and that the distribution of Na^+ in young and mature leaves were important part of such regulation (Shannon et al. 1987). In a more recent study, however, no relationship was observed between tissue ion content and plant ST in BC populations of a cross between a tomato breeding line and a salt-tolerant accession (LA722) of *L. pimpinellifolium* (Foolad and Chen 1999). The overall conclusion from the various studies is that tissue ion content per se may not be a universal indicator of ST across tomato genotypes.

In tomato genotypes with glycophytic response to salinity, as ion concentration increases beyond a threshold level the exclusion mechanism fails and further increases in ion concentration in the root zone would result in fading plant growth and gradual death (Foolad 1997; Perez-Alfocea et al. 1993a). Thus, such genotypes may only be useful for cultivation under low to moderate levels of salt. At higher SS levels, genotypes that exhibit a halophytic response may be more advantageous. Unfortunately, however, many salt-tolerant wild accessions of tomato that exhibit a halophytic response to salinity often grow extremely slowly under SS with limited fruit production (Foolad 1996a; Tal 1997). Whether these associations are due to pleiotropic effects of the same genes or undesirable linkage between different genes is unknown. Several studies in tomato and other plant species have suggested that genes contributing to plant vigor are different from those conferring ST, and when breeding for efficient production under saline conditions genes for both plant vigor and ST are important (Foolad 1996a; Forster et al. 1990). This may limit the utility of wild accessions with halophytic response to salinity for breeding tomatoes with enhanced ST. However, further studies are needed to verify this conclusion.

2.3.2.   *Inheritance of salt tolerance during vegetative stage*

Genetics research on tomato ST during VS started about 3 decades ago, when Emanuel Epstein proposed exploitation of gene resources within the wild *Lycopersicon* species to increase ST of the cultivated tomato (Epstein et al. 1980; Rush and Epstein 1976). Subsequently, hybridizations were made between a salt-tolerant accession (LA1401) of *L. cheesmanii* and a salt-sensitive tomato cultivar and filial and BC progeny were produced (Rush and Epstein 1981a). The authors reported that selection in the segregating populations led to progeny with enhanced ST, suggesting that ST of LA1401 could be transferred to the cultivated tomato. Although no salt-tolerant cultivar was derived from these materials, this study led to other investigations of genetics and breeding of ST in tomato. (Saranga et al. 1992) developed BC populations of a cross between a salt-sensitive tomato line and a salt-tolerant accession (LA716) of *L. pennellii* and evaluated them for tolerance under saline field conditions. Estimates of h^2 for total dry matter and total fruit yield under saline conditions as well as total dry matter under salt relative to control conditions were moderate (0.3–0.45), suggesting

that ST of the cultivated tomato could be improved by using LA716 as a gene resource. However, there has not been any report of a salt-tolerant cultivar derived from these materials. By evaluating F_2 progeny of a cross between a salt-sensitive tomato and a salt-tolerant accession of *L. pimpinellifolium* under SS, (Asins et al. 1993b) concluded that total fruit yield and fruit number were useful selection criteria for improving tomato ST; estimates of broad-sense h^2s for these traits were 0.53 and 0.73, respectively. In a greenhouse hydroponics study, using parental, filial and BC populations of an intraspecific cross between a salt-sensitive tomato breeding line and a salt-tolerant primitive cultivar (PI174263), it was determined that growth under SS relative to control, the most widely used index in physiological investigation of ST in tomato, was under additive genetic control and could be a possible selection criterion for improving tomato ST (Foolad 1996a). In none of the aforementioned studies, however, was any empirical selection made to verify the suggestion that ST of tomato could be improved by directional PS. Nonetheless, these and other studies (Bolarin et al. 1991; Foolad 1996a) have suggested that shoot growth under salinity relative to control (a.k.a. relative growth under SS) should be the best indicator of ST, which may be useful in ST breeding in tomato.

2.3.3.   *Physiological genetics of salt tolerance during vegetative stage*

Direct selection for ST under field conditions is generally difficult because of confounding effects of numerous other environmental factors (Richards 1983; Yeo and Flowers 1990). A suggested approach to improve the efficiency of selection for ST has been the adoption of new selection criteria based on knowledge of physiological processes which limit crop production under saline conditions (Flowers and Yeo 1988, 1997; Tal 1985; Yeo and Flowers 1990). Physiological criteria that have been suggested as potential indicators of ST in tomato include tissue water potential, tissue ion content, K^+/Na^+ ratio, osmoregulation, succulence, and water use efficiency (WUE) (Asins et al. 1993b; Foolad 1996a, 1997; Guerrier 1996; Martin and Thorstenson 1988; Perez-Alfocea et al. 1993b; Romero-Aranda et al. 2001; Saranga et al. 1993). However, whether these physiological parameters are good indicators of ST in tomato, or if there are genetic variations in these responses, must be determined before assessing their utility as indirect selection criteria for improving tomato ST.

Genetic research to examine the value of physiological parameters for breeding for ST in tomato has been scarce. In one study, analysis of the parental, filial and BC generations of an intraspecific cross between a salt-sensitive tomato line and a salt-tolerant primitive cultivar (PI174263) indicated that growth under SS was positively correlated with leaf Ca^{2+} content and negatively correlated with leaf Na^+ content (Foolad 1997). Generation means analysis of these populations indicated that accumulations of both Na^+ and Ca^{2+} in the leaf under SS were genetically controlled with additivity being the major genetic component. Tissue ion concentration was therefore suggested as a useful selection criterion when breeding for improved ST of tomato using PI174263 as a genetic source (Foolad 1997). As discussed in section 2.3.1., a few other studies have speculated on the utility

of physiological parameters as indirect selection criteria for breeding salt-tolerant tomatoes (Asins et al. 1993b; Cuartero et al. 2006; Foolad 1997; Saranga et al. 1993; Tal and Gavish 1973; Tal et al. 1979). However, despite these studies, there is yet no consensus on what might be the best physiological or morphological characteristic(s) that should be employed as indirect selection criteria when breeding tomatoes for ST. Most likely a combination of different characteristics should be considered if salt-tolerant genotypes with commercial values are expected. This, by itself, indicates the complexity of ST and the need for identifying better approaches for characterizing genetic bases of tolerance components to facilitate development of commercial cultivars with enhanced ST. Recent advances in molecular marker technology, QTL mapping, MAS, and genetic transformation have provided some promising approaches.

2.3.4. *QTL analysis of salt tolerance during vegetative stage*

A few studies have identified QTLs for ST during VS in tomato. In one study, a BC_1S_1 population of a cross between a tomato breeding line and a salt-tolerant accession of *L. pimpinellifolium* (LA722) was screened for ST (Foolad and Chen 1999). The two parents were distinctly different in ST: while 80% of LA722 survived after two weeks under a salt concentration of 700 mM NaCl + 70 mM $CaCl_2$ (equivalent to $\sim$64 dSm^{-1}), only 25% of the *L. esculentum* line remained alive. The BC_1S_1 population exhibited a continuous variation, with survival rate ranging from 9% to 94% across families. Interval mapping identified five QTLs for ST on tomato chromosomes 1, 3, 5 and 9. All QTLs had the positive alleles from *L. pimpinellifolium*. The results supported the previous suggestion (Foolad 1996a, 1997) that ST during VS in tomato was controlled by more than one gene. However, the involvement of only a few QTLs, which accounted for a large portion of the total phenotypic variation, suggested utility of MAS for transferring ST QTLs from LA722 to the cultivated tomato. Analyses of leaf Na^+, K^+, Mg^{2+}, Ca^{2+}, Cl^-, $NO3^-$, $SO4^{2-}$ and $PO4^{3-}$ contents indicated the absence of a correlation between ST and tissue ion content in this population; no QTL was identified for tissue ion content under SS. Using a different BC population of the same cross, a selective genotyping approach was used to verify the previously-identified QTLs and possibly identify new QTLs (Foolad et al. 2001). In this study, from a population of 792 BC_1 plants grown under SS, 37 most salt-tolerant individuals were selected and grown to maturity and produced BC_1S_1 seeds. The 37 selected BC_1S_1 families and 119 nonselected (random) BC_1S_1 families were evaluated for ST and their performances compared. A realized h^2 of 0.46 was obtained for ST during VS, consistent with a previous estimate of h^2 for this trait obtained from an intraspecific cross of tomato (Foolad 1996a). A trait-based marker analysis (selective genotyping) led to the detection of five QTLs for ST on chromosomes 1, 3, 5, 6 and 11 (Foolad et al. 2001). Except for one, all QTLs had positive alleles contributed from the salt-tolerant *L. pimpinellifolium* parent. Three of the five QTLs were at the same locations as those identified in the first study (Foolad and Chen 1999). The high level of consistency between results of the two studies indicated the genuine nature

of the detected QTLs and their potential utility for ST breeding using MAS. In each of these two studies, a few individuals were identified with most or all of the QTLs and with a ST comparable to that of the salt-tolerant *L. pimpinellifolium* accession for future ST breeding.

In a more recent study, 145 F_9 recombinant inbred lines (RILs) of a *L. esculentum* × *L. pimpinellifolium* cross were evaluated in replicated trials for ST during VS. The RILs were genotyped for 129 RFLP and 62 resistance gene analog (RGA) markers, covering 1,505 cM of tomato genome with an average marker distance of 7.9 cM. Interval analysis identified 7 QTLs for ST during VS on tomato chromosomes 3, 4, 5, 7, 8, 9 and 12 (M.R. Foolad et al., unpubl. data). The QTLs detected on chromosomes 3, 5, and 9 were the same as those identified in the previous studies and exhibited larger effects than the newly identified QTLs on chromosomes 4, 7, 8 and 12. The overall results from these three studies indicated that the stable QTLs on chromosomes 3, 5 and 9 should be useful for introgression into the cultivated tomato via MAS to improve tomato ST during VS. However, further studies are needed to verify these QTLs in other genetic backgrounds or identify new QTLs for gene pyramiding and development of tomatoes with enhanced ST during VS.

2.4. Salt Tolerance During Reproduction

Much less research has been conducted on tomato ST during reproduction than earlier stages. In particular, little effort has been devoted to determine pollen viability or stigma receptivity, and/or the ability of the plant to produce flowers or set fruit under SS. This may be due in part to a higher level of ST generally observed during reproduction than earlier stages in tomato. For example, increasing salinity to 10 dSm^{-1} did not significantly affect fruit set in tomato, which was reduced only at 15 dSm^{-1} (Adams and Ho 1992). Also, it was reported that salinity did not affect tomato pollen viability, though the number of pollen grains per flower decreased with the duration of salinity (Grunberg et al. 1995). In a recent study, 13 tomato accessions from 3 different species were grown under saline (300 mM NaCl + 30 mM CaCl$_2$; equivalent to $\sim$ 28 dSm^{-1}) and control conditions and their pollen production and *in-vitro* pollen germination were examined (S Prakash and MR Foolad, unpubl. data). For most accessions, there was no significant reduction in pollen production (per flower) in response to SS. Pollens from both salt-grown and control-grown plants were cultured at different SS levels, including 0, 0.2, 0.4 and 0.8% NaCl, and evaluated for percentage germination after 4 or 8 h of incubation. In all accessions, pollen germinability was decreased under salt compared to control treatment, and the reduction was greater at higher (0.8%) than lower (0.2%) salt concentrations. However, in most accessions, *in-vitro* pollen germinability of salt-grown plants was generally higher than that of the control-grown plants, suggesting that pollen ST was increased by growing plants under SS.

In the cultivated tomato, fruit yield generally starts decreasing when the EC of the saturated soil extract exceeds 2.5 dSm^{-1} (Maas 1990; Saranga et al. 1991), though

there are reports of higher thresholds for yield reduction in tomato (Adams 1991). A 10% reduction in fruit yield is expected per additional dSm^{-1} beyond the threshold level (Saranga et al. 1991). The major cause of yield reduction in tomato under low to moderate levels of salinity (EC = 3–9 dSm^{-1}) is the reduction in the average fruit size, and not a reduction in fruit number (van Ieperen 1996). A 10% reduction in fruit size is caused following irrigation with 5–6 dSm^{-1} water, a 30% reduction with 8 dSm^{-1}, and about 50% reduction at 9 dSm^{-1} (Cuartero and Fernandez-Munoz 1999). Thus, small-fruited genotypes, including cherry tomatoes, may be more successful than large-fruited ones when grown under low to moderate salinity (Caro et al. 1991). However, at higher levels of salinity, or prolonged exposure to salinity, a reduction in the total number of fruits per plant is the major cause of yield reduction, thus affecting both large-fruited and small-fruited genotypes (Cuartero and Fernandez-Munoz 1999; van Ieperen 1996). It is notable that the potential of tomato wild species as sources of ST during reproduction has not been assessed critically, mainly because most of the wild accessions are self-incompatible and/or produce very small fruits and thus cannot be easily compared with the cultivated tomato. However, progenies derived from interspecific crosses have often been used for salt tolerance studies.

Limited research has been conducted to identify genes or QTLs for ST during reproduction in tomato. In one study, using 14 genetic markers and an F_2 population of a cross between a salt-sensitive cultivar and a salt-tolerant *L. pimpinellifolium* accession, a few QTLs were detected affecting fruit yield, fruit number and fruit size under SS. However, because of the extreme difference in fruit size between the parents of the F_2 population, it is likely that QTL effects were confounded by effects of genes controlling fruit size. Similar studies were conducted in F_2 populations of different crosses between *L. esculentum* and either *L. pimpinellifolium* or *L. cheesmanii*, and several other QTLs were reported for the same fruit-related traits (Monforte et al. 1996, 1997, 1999). However, large differences between parental lines of these populations, including differences in flowering habits, maturity time, fruit size, fruit number and total fruit yield, would have adversely affected the power of the experiments in detecting true QTLs affecting ST. Therefore, the identified QTLs should be validated using advanced generations before they are employed in MAS. In conclusion, more comprehensive studies are needed to carefully identify genetic factors (QTLs) which truly contribute to ST during reproduction in tomato and which could be used for marker-assisted breeding.

2.5. Relationship Among Salt Tolerance at Different Developmental Stages

Knowledge of genetic relationships among tolerance at different developmental stages is necessary to facilitate development of cultivars with enhanced ST throughout the plant ontogeny. Early studies had suggested absence of phenotypic relationships among different stages of plant development in regard to ST in various plant species (Abel and Mackenzie 1963; Greenway and Munns 1980; Johnson et al. 1992). In

tomato, recently systematic approaches were taken to examine phenotypic as well as genetic relationships among tolerance to salinity in different developmental stages. In one study, an F_4 population of a cross between a salt-nsensitive tomato breeding line and a primitive cultivar (PI174263) with ST during both SG and vegetative stages was evaluated for tolerance during both stages. In the F_4 population, there were significant variation among families in terms of ST during both SG and VS, however, there was no significant correlation ($r_p = -0.10$, $P > 0.05$) between ST during the two stages (Foolad and Lin 1997a). To examine the genetic correlation between ST during SG and VS, selection was made for rapid SG under SS in an F_2 population of the same cross and the selected F_3 progeny were evaluated for ST separately during both SG and VS. The results indicated that while selection improved germination ST of the F_3 progeny significantly, it did not affect ST of the F_3 progeny during VS, suggesting that genetic and physiological mechanisms that contributed to ST during SG were different from those conferring ST during VS (Foolad and Lin 1997a). This relationship was further examined by comparison of QTLs affecting ST during each of the two stages (Foolad 1999). Using a BC_1S_1 population of a cross between a salt-sensitive tomato line and a *L. pimpinellifolium* accession (LA722) with ST during both SG and VS, it was determined that QTLs for ST during SG were different from QTLs for ST during VS. A similar QTL study was recently conducted using 145 F_9 RILs of the same cross, and the results supported the previous finding of absence of a genetic relationship between ST during SG and VS (MR Foolad et al., unpubl. data). The overall results indicated that ST during SG in tomato was independent of ST during VS, consistent with earlier reports that ST of young tomato plants did not correlate with that of mature plants (Shannon et al. 1987) and that ST ranking of tomato genotypes based on vegetative characteristics differed from the ranking based on fruit yield (Caro et al. 1991).

Absence of genetic relationships in ST among different developmental stages have also been reported in other plant species, including alfalfa, *Medicago sativa* L. (Johnson et al. 1992), barley (Mano and Takeda 1997), Arabidopsis (Quesada et al. 2002), wheat, *Triticum aestivum* L. (Ashraf and McNeilly 1988), triticale, *Triticale hexaploide* Lart. (Norlyn and Epstein 1984), and slender wheatgrass, *Elymus trachycalus* spp. *Trachycalus* (Link) Malte (Pearen et al. 1997). Findings from different studies suggest that when breeding for improved ST, each stage of plant development must be evaluated separately for assessment of tolerance and identification, characterization and utilization of useful genetic components. However, identification of QTLs for ST at different developmental stages may facilitate pyramiding of tolerance factors and development of cultivars with improved ST at all stages.

2.6.   Transgenic Approaches to Develop Salt Tolerant Tomatoes

Many genes are involved in a plant's response to SS, which may lead to a wide variety of biochemical and physiological changes. These include expression of genes that facilitate compartmentalization of toxic ions in the vacuoles, activation of detoxifying enzymes, synthesis of late-embryogenesis-abundant (LEA) proteins,

and accumulation of compatible solutes. Genetic engineering approaches to developing stress-tolerant plants are considered an attractive alternative to conventional breeding protocols. Recently, transgenic approaches have been employed to produce plants with enhanced tolerance to various abiotic stresses, including salinity, by overexpression of genes controlling different tolerance-related physiological mechanisms (Bajaj et al. 1999; Bartels and Sunkar 2005; Chinnusamy et al. 2005; Rontein et al. 2002; Seki et al. 2003; Serrano et al. 1999; Wang et al. 2003; Yamaguchi and Blumwald 2005; Zhang et al. 2004). For example, plants have been engineered with genes encoding enzymes that enhance the synthesis of compatible solutes such as mannitol (Thomas et al. 1995), glycine betaine (Lilius et al. 1996), proline (Zhu et al. 1997) and polyamines (Galston et al. 1997), which contribute to osmoregulation and improving plant stress tolerance (Rathinasabapathi 2000; Rontein et al. 2002). Compatible solutes may also contribute to stress tolerance through other functions such as protection of enzyme and membrane structure and scavenging of radical oxygen species (Bohnert and Shen 1999; Rathinasabapathi 2000; Shen et al. 1997; Wang et al. 2003). Transgenic plants also have been produced with overexpression of different vacuolar antiport proteins, which facilitate exclusion of toxic ions from the cell cytosol (Apse et al. 1999; Apse and Blumwald 2002; Serrano et al. 1999; Wang et al. 2003; Yamaguchi and Blumwald 2005; Zhang and Blumwald 2001; Zhang et al. 2001a). Furthermore, transgenic plants have been developed with increased expression of detoxification enzymes, which reduce oxidative stress (Tanaka et al. 1999). Although in almost all cases growth of transgenic plants were examined under controlled conditions and their performance under field were unknown, the transgenic approach has facilitated a better understanding of the mechanisms leading to stress tolerance.

Despite considerable efforts in the area of genetic transformation, limited attempts have been made to develop transgenic tomatoes with enhanced ST. A notable progress has been development of tomato plants overexpressing *AtNHX1*, a single-gene controlling vacuolar Na^+/H^+ antiport protein, introduced from *Arabidopsis thaliana* (Apse and Blumwald 2002; Yamaguchi and Blumwald 2005; Zhang and Blumwald 2001). The overexpression of this gene was previously shown to improve ST in *Arabidopsis* (Apse et al. 1999). Transgenic tomato plants overexpressing this gene were reported to have the ability to grow, set flower and produce fruit in the presence of 200 mM NaCl in greenhouse hydroponics whereas the control plants did not survive the saline conditions. The transgenic plants were reported to have acquired a halophytic response to SS, accumulating salts in the vacuoles. This is unlike the normal response of the cultivated tomato to SS, which is exclusion of salts from cells at the root shoot level, a glycophytic response. Accordingly, under high salinity conditions, transgenic tomato plants accumulated high concentrations of Na^+ and Cl^- in their leaves (Apse et al. 1999). The overproduction of the vacuolar Na^+/H^+ antiport protein enhanced the ability of the transgenic plants to sequester Na^+ in their vacuoles, averting its toxic effects in the cell cytosol. At the same time Na^+ was used to maintain an osmotic balance to drive water into the cell, and thus used salty water for cell expansion and growth. This was the first

reported example of a single-gene transformation in any crop species that resulted in such a significant enhancement in plant ST. Subsequently, however, transfer and overexpression of the same gene in canola, *Brassica napus* (Zhang et al. 2001a), corn (Yin et al. 2004) and wheat (Xue et al. 2004) resulted in transgenic plants with enhanced ST under controlled saline conditions. However, the transgenic plants are yet to be evaluated for ST under field conditions and examined for their commercial value. To date, there is no report of such studies. Obviously, much more research is needed to gain a better understanding of the genetics, biochemical, and physiological basis of plant ST using the transformation technology. However, knowledge of various tolerance components and identification, cloning and characterization of responsible genes may allow development of plants harboring multiple transgenes and production of highly salt-tolerant transgenic plants. With the recent advances in molecular biology of stress tolerance in tomato, this expectation may not be unlikely.

3. GENETICS OF AND BREEDING FOR DROUGHT TOLERANCE IN TOMATO

3.1. Background

Drought, defined as the occurrence of a substantial water deficit in the soil or in the atmosphere, is an increasingly important constraint to crop productivity and yield stability worldwide (Ceccarelli and Grando 1996). It is by far the leading environmental stress in agriculture. The worldwide losses in yield due to drought probably exceed the losses from all other causes combined (Blum 1988; Kramer 1980; Schonfeld et al. 1988). In the U.S., up to 45% of the land surface is subject to continuous or frequent water stress (Boyer 1982; Tanji 1990) and a drought occurs somewhere in the country every year, costing billions of dollars in damage to crops and businesses (Ross and Lott 2000).

Most crop plants, including tomato, are sensitive to drought stress (DS) throughout the ontogeny of the plant, from SG to harvest (Hsiao 1973). Plant response to DS can be generally classified into three categories, drought escape, dehydration avoidance, and dehydration tolerance (Blum 1988; Kramer 1983). Drought escape includes situations where plants with short growth cycle and early maturity avoid experiencing drought. Breeding for drought escape should therefore be directed toward developing cultivars with early maturity so that by the time drought occurs the plant has already completed its life cycle. Dehydration avoidance is defined as the ability of the plant to retain a relatively higher level of "hydration" during the period of water stress (Blum 1988). In this situation, the plant protects its various growth related physiological, biochemical, and metabolic processes from the external water stress. A common measure of dehydration avoidance is the maintenance of a higher tissue water or turgor potential under conditions of water stress. Osmotic adjustment, as a means for retaining a higher turgor at a given tissue water potential, is an example of dehydration avoidance at the cell

level. When the tissue is not protected by any of the avoidance mechanisms, cells lose turgor and dehydrate, resulting in various cellular physicochemical injuries (Hsiao and Bradford 1983). Complete loss of free water will result in desiccation or dehydration. In general, however, different genotypes exhibit different responses to cellular and whole plant stresses caused by dehydration, and there are varying levels of dehydration tolerance. It should also be noted that characteristics of the three categories of plant response to DS are not generally independent of each other, and some plants may exhibit a combination of characteristics (Blum 1988).

A complementary approach in agricultural methods currently followed is to minimize losses incurred by water stress and develop "drought tolerant" cultivars with the ability to escape, avoid, and/or tolerate effects of water stress. However, despite many decades of research on drought tolerance (DT), till date drought stress continues to be a major challenge to plant breeders. This is in part due to the complexity of the trait. Accumulating evidence suggests that plant response to DS is controlled by many genes and physiological mechanisms (Blum 1988; Subudhi et al. 2000; Zhang et al. 2001b; Zhu et al. 1997) and varies depending on the influence of other environmental factors (Ceccarelli and Grando 1996; Richards 1996). Selection and breeding for DT is also difficult because tolerance appears to be a developmentally-regulated, stage-specific phenomenon (Blum 1988; Ludlow and Muchow 1990; Mitchell et al. 1998; Richards 1996). Each stage may be considered as a separate trait and may require a different evaluation method. Furthermore, no reliable evaluation procedure is known that can effectively and efficiently be employed to identify drought-tolerant plants at different stages of development. These and other complexities have led to a limited success in developing drought-tolerant crop plants, including tomato.

In tomato, most commercial cultivars are sensitive to DS throughout the ontogeny of the plant, yet genotypic variation for DT exists within the cultivated (Wudiri and Henderson 1985) and related wild species such as *L. cheesmanii*, *L. chilense*, *L. pennellii*, *L. pimpinellifolium*, and *L. esculentum* var. *cerasiforme* (Martin et al. 1989; Pillay and Beyl 1990; Richards and Phills 1979; Rick 1973, 1978; Rick 1979b; Rick 1982; Yu 1972). The latter species, being native of coastal deserts of western South America, witness rainless long periods except for the occasional El Niño episodes of heavy rains. These species grow at habitats where condensation of dew and fog drip at night are the main source of moisture (Rick 1973). They are also remarkably capable of overcoming brief wilting. Only few formal studies have been conducted to screen for DT in tomato. In one study, (Rana and Kalloo 1990) evaluated 150 lines of cultivated and wild species of tomato under water-deficit conditions and identified a few *L. esculentum* genotypes and a few accessions of *L. pimpinellifolium* and *L. chilense* with DT attributes. In a recent study, Husain and Foolad (unpubl. data) screened over 120 tomato genotypes and identified a few wild accessions exhibiting considerable DT (described in below). However, very limited effort (Kahn et al. 1993; Martin et al. 1999; Pillay and Beyl 1990) has been devoted to characterization of the physiology or genetics of DT in tomato to

warrant breeding activities toward development of drought-tolerant tomatoes. This is unlike extensive research that has been conducted on DT in many other crop species, including rice (Nguyen et al. 1997; Zhang et al. 2001b), corn (Ribaut et al. 1997), sorghum, *Sorghum bicolor* L. Moench (Subudhi et al. 2000) and lettuce, *Lactuca sativa* L. (Johnson et al. 2000). Also, comparatively less research has been done on tomato DT than tomato tolerance to other abiotic stresses such as salinity and extreme temperatures. Here, the available information on germplasm resources and genetics of DT in tomato is reviewed and the prospect for developing drought-tolerant tomatoes is discussed.

3.2.   Drought Tolerance During Seed Germination

The ability of the seed to germinate rapidly and uniformly under DS is a desirable trait for direct seeding tomato crops. Successful establishment of direct-seeded crops, however, depends on successful SG and seedling emergence. Most commercial cultivars of tomato are sensitive to DS during SG, however, sources of tolerance have been identified within the related wild species of tomato, including *L. pennellii* and *L. pimpinellifolium* (M.R. Foolad et al, unpubl. data), and some studies have been undertaken to discern the genetic basis of DT during SG in tomato.

3.2.1.   Inheritance of drought tolerance during seed germination

The genetic basis of DT during SG in tomato has recently been studied using interspecific crosses between *L. pimpinellifolium* and *L. esculentum* (Foolad et al. 2003a; Foolad et al. 2003b; Subbiah 2001). In one study, for example, a BC_1 population (N = 1000) from a cross between a drought-tolerant *L. pimpinellifolium* accession (LA722) and a drought-sensitive tomato breeding line was evaluated for SG under DS (14% PEG, $\psi_w \approx -680$ kPa), and the most rapidly germinating seeds (first 3% germinated) were selected. The 30 selected BC_1 individuals were grown to maturity and self-pollinated to produce BC_1S_1 progeny seeds. Select BC_1S_1 progeny families were evaluated for germination under DS and their average performance was compared with that of a nonselected BC_1S_1 population of the same cross. Results indicated that selection for rapid SG under DS was effective and significantly improved progeny SG rate under DS; a realized h^2 of 0.41 was obtained for DT during SG in this population. The results indicated that DT during SG in tomato was genetically controlled and could be improved by PS.

3.2.2.   Mapping of QTLs for drought tolerance during seed germination

A few recent studies have identified QTLs for DT during SG in tomato. In one study, a trait-based marker analysis, using BC_1 individuals of a cross between a drought-sensitive tomato breeding line and a drought-tolerant *L. pimpinellifolium* accession (LA722), detected four QTLs on chromosomes 1, 4, 8, 9, and 12 for DT (Foolad et al. 2003b). The results indicated that DT during SG in tomato was a

quantitative trait, controlled by more than one gene. A few BC_1S_1 families were identified with most or all of the QTLs and with a DT comparable to that of LA722. These families should be useful for developing germination drought-tolerant tomato lines using MAS. In another study, 145 F_9 RILs of the same cross were evaluated for germination rate under DS and, by using composite interval mapping analysis, several QTLs for DT during SG were identified on tomato chromosomes 1, 2, 3, 4, 8, 9, and 12 (MR Foolad et al., unpubl. data). The results of this study were consistent with those of the previous one and suggested the presence of stable QTLs for DT during SG in populations derived from the *L. esculentum* × *L. pimpinellifolium* cross. These QTLs should be useful for improving tomato DT during SG using MAS.

3.3.   Drought Tolerance During Vegetative Growth and Reproduction

Potential sources of DT during vegetative growth and later stages in tomato have been identified among accessions of the wild species *L. chilense* and *L. pennellii* (Rick 1973, 1978; Rick 1979b; Rick 1982). Different tolerance indices (TIs) have been suggested or employed to characterize physiological and genetic bases of DT in tomato, including dry weight (DW) of shoot and root, root length, root morphology, leaf rolling, flower and fruit set, fruit weight, fruit yield, WUE, recovery after re-watering, stomatal resistance, plant survival, leaf water potential, leaf osmotic potential, osmoregulation, transpiration rate, photosynthetic rate, enzymatic activities (e.g. superoxide dismutase and Rubisco), and pollen viability and germination (Blum 1988; Cohen et al. 1991; Kalloo 1991; Lutfor-Rahman 1998; Martin and Thorstenson 1988; Pillay and Beyl 1990; Rana and Kalloo 1989; Richards and Phills 1979). In a germplasm screening study, for example, tomato cultivar Saladette was considered drought tolerant as determined by a smaller reduction in fruit set compared to other cultivars, which in turn was attributed to its ability to roll up leaves under a high evaporative demand and maintain a high leaf water potential (Wudiri and Henderson 1985). The physiological basis of DT in *L. chilense* was attributed to its deep vigorous root system (Rick 1978), similar to those reported for cultivar Red Rock (Stoner 1972) and a few accessions of *L. pimpinellifolium* (Rana and Kalloo 1989). In contrast to these findings, the "drought-tolerant" *L. pennellii* accession LA716 has a limited and shallow root system and the basis for its DT is largely due to the ability to conserve moisture in succulent leaves during periods of limited rainfall. Also, LA716 has been characterized as having a greater WUE under DS than *L. esculentum*, as measured by g DW produced per Kg of water consumed (Martin and Thorstenson 1988). A high WUE in this accession was attributed to smaller leaf conductance due to fewer and smaller stomata, longer trichomes, lower chlorophyll content and Rubisco activity per unit leaf area, and larger mesophyll cell surface exposed to intercellular air space (Martin et al. 1999). However, though WUE may be a good indicator of DT in tomato, its measurement under field condition is not without inherent difficulties. Thus, attempts have been

made to determine the relationship between WUE and stable carbon isotope discrimination (Δ), a measure of proportion of ^{13}C relative to ^{12}C in plant organic matter, which is easier to measure when dealing with large number of plants. (Martin et al. 1999) suggested that WUE in progeny of crosses between *L. esculentum* and *L. pennellii* LA716 could be increased by selecting for low Δ, however, this could lead to the selection of smaller plants, an agriculturally undesirable characteristic. The authors suggested that the small plant size could be corrected by conventional breeding following selection for DT, but no such effort has been reported.

Most recently a systematic study was conducted to identify sources of DT during vegetative stage in tomato (S Husain and MR Foolad, upbubl.). In this study, over 120 accessions from the cultivated tomato and wild species *L. pimpinellifolium*, *L. chilense*, *L. peruvianum* and *L. pinnellii* were screened in two treatments of control (no stress) and drought (stress) under greenhouse conditions. The growth parameters measured were shoot length, fresh and dry weight as well as root length and DW. TIs were also calculated as the ratio of growth under DS to growth under control conditions. The greenhouse experiments were repeated 3 times and similar parameters were measured. Based on absolute shoot DW under drought stress, *L. esculentum* genotypes exhibited the least DT. *L. pennellii* accessions were found to be the most drought tolerant, exhibiting greater shoot DW under stress and greater TIs, followed by *L. pimpinellifolium* accessions. As to the root DW under stress, *L. pimpinellifolium* accessions had the most root biomass accumulated followed by *L. peruvianum* accessions. Similar trend was observed as to the root length. An interesting observation was that *L. chilense* accessions showed the best performance as to TIs for the root length and root DW, followed *L. pennellii*, *L. peruvianum*, *L. pimpinellifolium* and *L. esculentum*. Overall this study identified some new accessions within the wild species of tomato with DT, which deemed to be better than those previously reported. These accessions should be useful for physiological and genetic studies, including mapping of tolerance-related genes/QTLs and their use in marker-assisted breeding.

3.3.1.   Inheritance and QTL mapping for drought tolerance during vegetative growth and reproduction

Very limited research has been conducted to characterize genetic controls of DT or develop tomatoes with improved tolerance. In one study, three QTLs associated with low Δ were identified using F_3 and BC_1S_1 progeny of a cross between a *L. esculentum* breeding line and *L. pennellii* accession LA716 (Martin et al. 1989). However, it was not determined whether selection for these QTLs would increase WUE in tomato. Other related studies on genetics of tomato DT during vegetative growth include identification of several genes or mRNAs whose expressions were reportedly elevated in response to DS. For example, four drought-induced genes, *le4*, *le16*, *le25* and *le20*, were identified and characterized in tomato (Cohen et al. 1991; Kahn et al. 1993; Plant et al. 1991). It was determined that the increase in expression of these genes occurred after a longer period of water deficit in

L. pennellii than in the cultivated tomato, although these genes did not appear to be responsible for DT in *L. pennellii* (Kahn et al. 1993). Overall, in tomato too few studies have been undertaken to characterize genetic controls of DT post germination stage and/or to warrant any type of breeding activities. Obviously DT has not been a pressing issue for tomato breeders or its complexity has deterred them of breeding attempts.

3.4.   Transgenic Approaches to Tomato Drought Tolerance

Very limited transgenic research has been done on tomato DT. This is unlike considerable research conducted in other plant species to identify, characterize and transfer genes toward development of drought-tolerant transgenic plants (Bajaj et al. 1999; Bartels and Sunkar 2005; Cherian et al. 2006; Grover et al. 1999; Kasuga et al. 2004; Oh et al. 2005; Serrano et al. 1999; Shou et al. 2004; Zhang et al. 2004). However, a few basic studies have been undertaken to investigate effects of selected foreign genes, in particular from Arabidopsis, on tomato response to water deficit. In one study, for example, transfer of an Arabidposis DNA cassette containing C repeat / dehydration-responsive element binding factor 1 (*CBF1*), under the control of CAMV35S promoter, resulted in transgenic tomatoes with water-deficit resistance greater than normal plants (Hsieh et al. 2002). In this study, however, it appeared that the introduced DNA had negative pleiotropic effects on plant growth under normal conditions such that fresh weight and fruit and seed numbers in transgenic plants were less than the isogenic wild-type plants. Further studies demonstrated that such negative effects were reversible by application of exogenous GA, which did not have any effect on plants' DT. In another study, transgenic tomato plants expressing CBF1 driven by an ABA-responsive complex (ABRC1) from the barley *HAV22* gene exhibited tolerance to DS, low temperature and SS; these plants maintained normal growth and yield under nonstress conditions (Lee et al. 2003). The results of this study suggested the potential benefit of using ABRC1-CBF1 transgenic tomato plants for production under stressful conditions. In a more recent study, (Na 2005) investigated the possibility of developing drought-tolerant tomatoes by developing transgenic plants containing either a tomato type I inositol 5 polyphosphatase (5PTse) or an ABRE binding factor ABF4 derived from Arabidopsis. While transgenic tomatoes containing the former gene exhibited some resistance to water deficit, they were retarded in growth. However, transgenic tomatoes expressing Arabidopsis ABF4/AREB2 exhibited more DT than non-transgenic plants, which was demonstrated to be due to lower water loss per unit leaf area. In another recent study, it was determined that transgenic tomato plants harboring the yeast trehalose-6-phosphate synthase (TPS1) gene under the control of CAMV35S promoter were more drought tolerant than the wild-type plants, though the transgenic plants exhibited some undesirable pleiotropic changes in plant morphology (Cortina and Culianez-Macia 2005). Overall, the results of these studies clearly demonstrate the potential utility of transgenic approaches to develop drought-tolerant tomatoes, though none of these investigations has led to

development of any agriculturally-acceptable stress-resistant cultivar. While there is a good prospect for developing transgenic tomato cultivars with improved DT, it seems fine-ntuning of this approach necessitates a lot more basic and applied research efforts.

4.   CURRENT STATUS AND FUTURE PROSPECTS
FOR DEVELOPING TOMATOES WITH SALT
AND/OR DROUGHT TOLERANCE

Most commercial cultivars of tomato are sensitive to salt and drought stresses during all stages of plant development, thus restricting tomato production in environments with such stresses. Occurrence of several genetic bottlenecks during tomato domestication and evolution, led the cultivated tomato to be depauparate in genetic diversity, including genes for abiotic stress tolerance. Fortunately, however, the related wild species of tomato are a rich source of desirable genes for tomato crop improvement. Although thus far only a superficial assessment of the extent of genetic variation for abiotic stress tolerance within *Lycopersicon* species has been made, some accessions with tolerance to salt or drought stress have been identified. Such resources have been utilized in physiological and genetic studies of salt and drought tolerance in tomato. However, more research is needed before commercial cultivars of tomatoes with the ability to grow and produce economic yield under saline or drought conditions will be available.

Absence of any tomato cultivar with proven field tolerance to salinity can be attributed to several factors including complexity of the trait, multifaceted interactions of ST with other agronomically important traits, insufficient understanding of the basic physiological and genetic mechanisms of ST, lack of efficient selection criteria, and, most importantly, limited efforts that has been devoted to identification, characterization and utilization of genetic resources for ST breeding. However, with the advent of new tools of plant molecular biology, including molecular marker technology and genetic transformation, the focus has largely been shifted to discerning genetic and physiological bases of ST in tomato, and some notable progress has been made. Recently, some tolerance components have been defined and their genetic controls characterized, and several controlling QTLs or genes with major effects have been identified and/or cloned. The new technology of gene transfer has provided opportunities to engineer tomatoes with enhanced ST using genes from unrelated species. Although transgenic plants have only been subjected to artificial laboratory tests of ST, the prospect for engineering tomato plants with field tolerance is improving. Furthermore, with our improved understanding of the significance of ST breeding in tomato, it is not unexpected to witness tomato cultivars with improved field ST in a near future. Notably, several research programs around the world, which are equipped with traditional and/or modern technologies of crop improvement, are currently working on development of tomatoes with enhanced ST.

Comparatively, however, much less progress has been made in genetics and breeding of tomatoes for DT. From the preceding discussion in this chapter, it is evident that currently there is limited physiological and/or genetic information on tomato DT to warrant development of cultivars with improved tolerance. Primarily, very limited knowledge is available as to genetic resources in *Lycopersicon* with DT attributes. Ironically, most tomato studies on DT have employed a single accession (LA716) of *L. pennellii* as a source of tolerance. However, due to various undesirable characteristics of this accession, in particular its extremely slow growth rate under DS, its usefulness as a genetic source for DT breeding in tomato is questionable. Although this accession can survive long periods of dryness, it lacks many other characteristics needed for use as a gene resource for DT breeding. Thus, initially larger germplasm screening experiments must be carried out including different wild species of tomato to identify useful sources of DT. In particular, collections from torrid areas should be examined for DT at different developmental stages.

Selection criteria for screening or breeding tomatoes for DT are also less clear than those available for ST breeding. More comprehensive studies are needed to identify and validate useful selection criteria, including morphological, agronomical, physiological, biochemical and molecular characteristics. In general, considering the normal climatic conditions for growing tomatoes, where short periods of drought may occur intermittently throughout the growing season, it seems that the ability of the tomato plant to survive transient periods of water stress and to recover rapidly upon re-availability of water is far more important than the ability to survive long-term water stress. Rather limited investigation has been done in this area in tomato, which deserve more attention. From a practical point of view, the most reliable criteria for breeding for DT are agronomic characteristics such as yield, and absolute and relative plant growth under stress and nonstress environments. Such criteria, however, may not be efficient or feasible to apply because in most initial germplasm evaluation or breeding projects often a large number of individuals, families or populations are screened, many of which may have wild genetic backgrounds. Alternative criteria based on physiological characteristics such as photosynthetic rates, stomatal resistance and leaf water potential might be more efficient. These characteristics are easier to measure, compared to yield, and generally show good correlations with agronomic characteristics. However, such characteristics must be identified and verified for specific sources of tolerance. Other selection criteria include biochemical characteristics such as enzyme activities and protein contents. These characteristics, however, often show weak correlations with agronomic traits and are expensive to measure. Additional options include identification and utilization of molecular markers associated with tolerance-related physiological, morphological or agronomic characteristics. Limited research has been conducted in this area in tomato. Transgenic approaches, which have been employed in several other plant species to increase DT, may also be useful for developing tomatoes with improved DT. This approach may require identification, examination and utilization of DT-related genes or proteins across species. In

general, however, if tomato cultivars for commercial production under DS conditions are desired, it may be necessary to create and employ innovative combinations of germplasms, trait characteristics, tolerance criteria, and technologies at different stages of the breeding process.

In summary, to facilitate development of tomatoes with improved salt or drought tolerance, the following recommendations are made:

1. Conduct large screening experiments to identify highly desirable sources of genetic tolerance, in particular in relation to DS.
2. Identify and characterize major components of tolerance at different developmental stages. Often it is not only one physiological mechanism or genetic factor that contributes to plant stress tolerance throughout its ontogeny. Also, different physiological or genetic mechanisms of tolerance may be involved in different genetic backgrounds. Identification and characterization of individual components of genetic tolerance may simplify the breeding process and allow pyramiding of tolerance components across developmental stages and genetic backgrounds.
3. Extend the search for identification and utilization of potential tolerance components, including genes and proteins, beyond the limits of species within *Lycopersicon*, and possibly include other genera, including model plants and microbial organisms.
4. Establish interdisciplinary collaborations among plant physiologists, geneticists, breeders and molecular biologists interested in stress tolerance. Successful development of commercial cultivars with proven tolerance under field conditions is beyond the capabilities of one individual scientist or laboratory.

REFERENCES

Abel GH, Mackenzie AJ (1963) Salt tolerance of soybean varieties (*Glycine max* L. Merrill) during germination and later growth. Crop Sci 3:159–161

Adams P (1991) Effects of increasing the salinity of the nutrient solution with major nutrients or sodium chloride on the yield, quality and composition of tomatoes grown in rockwool. J Hort Sci 66:201–207

Adams P, Ho LC (1992) The susceptibility of modern tomato cultivars to blossom-end rot in relation to salinity. J Hort Sci 67:827–839

Apse MP, Aharon GS, Snedden WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vaculolar Na/H anitort in *Arabidopsis*. Science 285:1256–1258

Apse MP, Blumwald E (2002) Engineering salt tolerance in plants. Curr Opin Biotech 13:146–150

Arumuganathan K, Earle ED (1991) Nuclear DNA content of some important plant species. Plant Mol Biol Rep 9:208–218

Ashraf M, McNeilly T (1988) Variability in salt tolerance of nine spring wheat cultivars. J Agron Crop Sci 160:14–21

Asins MJ, Breto MP, Cambra M, Carbonell EA (1993a) Salt tolerance in *Lycopersicon* species. I. Character definition and changes in gene expression. Theor Appl Genet 86:737–743

Asins MJ, Breto MP, Carbonell EA (1993b) Salt tolerance in *Lycopersicon* species. II. Genetic effects and a search for associated traits. Theor Appl Genet 86:769–774

Bajaj S, Targolli J, Liu LF, Ho THD, Wu R (1999) Transgenic approaches to increase dehydration-stress tolerance in plants. Mol Breed 5:493–503

Bartels D, Sunkar R (2005) Drought and salt tolerance in plants. Crit Rev Plant Sci 24:23–58

Bliss FA, Platt-Aloia KA, Thomson WW (1986) Osmotic sensitivity in relation to salt sensitivity in germinating barley seeds. Plant Cell Environ 9:721–725

Blum A (1988) Plant Breeding for Stress Environment. CRC Press, Boca Raton

Bohnert HJ, Shen B (1999) Transformation and compatible solutes. Scientia Hort 78:237–260

Bolarin MC, Fernandez FG, Cruz V, Cuartero J (1991) Salinity tolerance in four wild tomato species using vegetative yield-salinity response curves. J Am Soc Hort Sci 116:286–290

Bolarin MC, Perez-Alfocea F, Cano EA, Estan MT, Caro M (1993) Growth, fruit yield, and ion concentration in tomato genotypes after pre- and post-emergence salt treatments. J Am Soc Hort Sci 118:655–660

Boyer JS (1982) Plant Productivity and environment. Science 218:443–448

Bradford KJ (1986) Manipulation of seed water relations via osmotic priming to improve germination under stress conditions. HortScience 21:1105–1112

Bradford KJ (1995) Water relations in seed germination. In: Kigel J, Galili G (eds) Seed Development and Germination. Marcel Dekker, Inc., New York, pp 351–396

Breto MP, Asins MJ, Carbonell EA (1993) Genetic variablility in *Lycopersicon* species and their genetic relationships. Theor Appl Genet 86:113–120

Cano EA, Perez-Alfocea F, Moreno V, Caro M, Bolarin MC (1998) Evaluation of salt tolerance in cultivated and wild tomato species through *in vitro* shoot apex culture. Plant Cell, Tissue and Organ Cult 53:19–26

Caro M, Cruz V, Cuartero J, Estan MT, Bolarin MC (1991) Salinity tolerance of normal-fruited and cherry tomato cultivars. Plant and Soil 136:249–255

Ceccarelli S, Grando S (1996) Drought as a challenge for the plant breeder. Plant Growth Regul 20:149–155

Cherian S, Reddy MP, Ferreira RB (2006) Transgenic plants with improved dehydration-stress tolerance: progress and future prospects. Biol Plant 50:481–495

Chinnusamy V, Jagendorf A, Zhu J-K (2005) Understanding and improving salt tolerance in plants. Crop Sci 45:437–448

Choudhuri GN (1968) Effect of soil salinity on germination and survival of some steppe plants in Washington. Ecology 49:465–471

Cohen A, Plant AL, Moses MS, Bray EA (1991) Organ-specific and environmentally regulated expression of two absicisic acid-induced genes of tomato. Plant Physiol 97:1367–1374

Cook RE (1979) Patterns of juvenile morbidity and recruitment in plants. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) Topics in plant population biology. Columbia University Press, Los Angeles, pp 207–301

Cortina C, Culianez-Macia FA (2005) Tomato abiotic stress enhanced tolerance by trehalose biosynthesis. Plant Sci 169:75–82

Cuartero J, Bolarin MC, Asins MJ, Moreno V (2006) Increasing salt tolerance in the tomato. J Exp Bot 57:1045–1058

Cuartero J, Fernandez-Munoz R (1999) Tomato and salinity. Scientia Hort 78:83–125

Cuartero J, Yeo AR, Flowers TJ (1992) Selection of donors for salt-tolerance in tomato using physiological traits. New Phytol 121:63–69

Dahal P, Bradford KJ, Jones RA (1990) Effects of priming and endosperm integrity on seed germination rates of tomato genotypes: I. Germination at suboptimal temperature. J Expt Bot 41:1431–1440

Dehan K, Tal M (1978) Salt tolerance in the wild relatives of the cultivated tomato: Responses of *Solanum pennellii* to high salinity. Irrig Sci 1:71–76

Duvick DN (1986) Plant breeding: past achievement and expectations for the future. Econ Bot 40:289–294

Epstein E, Norlyn JD, Rush DW, Kingsbury RW, Kelly DB, Gunningham GA, Wrona AF (1980) Saline culture of crops: A genetic approach. Science 210:399–404

Esau K (1953) Plant Anatomy. John Wiley, New York

FAOSTAT (2005) FAO Statistical Databases. Food and agriculture organization of the United Nations, Statistics Division

Flowers TJ, Yeo AR (1988) Salinity and Rice: a physiological approach to breeding for resistance. The International congress of Plant Physiology, New Delhi, India, pp 953–959

Flowers TJ, Yeo AR (1997) Breeding for salt resistance in plants. In: Jaiwal PK, Singh RP, Gulati A (eds) Strategies for improving salt tolerance in higher plants. Science Publishers, Inc., U.S.A., pp 247–264

Foolad MR (1996a) Genetic analysis of salt tolerance during vegetative growth in tomato, *Lycopersicon esculentum* Mill. Plant Breed 115:245–250

Foolad MR (1996b) Response to selection for salt tolerance during germination in tomato seed derived from P.I. 174263. J Am Soc Hort Sci 121:1006–1011

Foolad MR (1997) Genetic basis of physiological traits related to salt tolerance in tomato, *Lycopersicon esculentum* Mill. Plant Breed 116:53–58

Foolad MR (1999) Comparison of salt tolerance during seed germination and vegetative growth in tomato by QTL mapping. Genome 42:727–734

Foolad MR (2004) Recent advances in genetics of salt tolerance in tomato. Plant Cell, Tiss Org Cult 76:101–119

Foolad MR, Chen FQ (1998) RAPD markers associated with salt tolerance in an Interspecific cross of tomato (*Lycopersicon esculentum* ∞ *L. pennellii*). Plant Cell Rep 17:306–312

Foolad MR, Chen FQ (1999) RFLP mapping of QTLs conferring salt tolerance during vegetative stage in tomato. Theor Appl Genet 99:235–243

Foolad MR, Chen FQ, Lin GY (1998) RFLP mapping of QTLs conferring salt tolerance during germination in an interspecific cross of tomato. Theor Appl Genet 97:1133–1144

Foolad MR, Jones RA (1991) Genetic analysis of salt tolerance during germination in *Lycopersicon*. Theor Appl Genet 81:321–326

Foolad MR, Jones RA (1992) Parent-offspring regression estimates of heritability for salt tolerance during germination in tomato. Crop Sci 32:439–442

Foolad MR, Jones RA (1993) Mapping salt-tolerance genes in tomato (*Lycopersicon esculentum*) using trait-based marker analysis. Theor Appl Genet 87:184–192

Foolad MR, Lin GY (1997a) Absence of a relationship between salt tolerance during germination and vegetative growth in tomato. Plant Breed 116:363–367

Foolad MR, Lin GY (1997b) Genetic potential for salt tolerance during germination in Lycopersicon species. HortScience 32:296–300

Foolad MR, Stoltz T, Dervinis C, Rodriguez RL, Jones RA (1997) Mapping QTLs conferring salt tolerance during germination in tomato by selective genotyping. Mol Breed 3:269–277

Foolad MR, Subbiah P, Kramer C, Hargrave G, Lin GY (2003a) Genetic relationships among cold, salt and drought tolerance during seed germination in an interspecific cross of tomato. Euphytica 130:199–206

Foolad MR, Zhang L, Subbiah P (2003b) Genetics of drought tolerance during seed germination in tomato: Inheritance and QTL mapping. Genome 46:536–545

Foolad MR, Zhang LP, Lin GY (2001) Identification and validation of QTLs for salt tolerance during vegetative growth in tomato by selective genotyping. Genome 44:444-454

Forster BP, Phillips MS, Miller TE, Baird E, Powell W (1990) Chromosome location of genes controlling tolerance to salt (NaCl) and vigor in *Hordeum vulgare* and *H. chilense* . Heredity 65:99–107

Galston AW, Kaur-Sawhney R, Altabella T, Tiburcio AF (1997) Plant polyamines in reproductive activity and response to abiotic stress. Bot Acta 110:197–207

Giovannucci E (1999) Tomatoes, tomato-based products, lycopene, and cancer; Review of the epidemiologic literature. J Natl Cancer Inst 91:317–331

Greenway H, Munns R (1980) Mechanism of salt tolerance in non-halophytes. Ann Rev Plant Physiol 31:149–190

Groot SPC, Karssen CM (1987) Gibberellins regulate seed germination in tomato by endosperm weakening: A study with gibberellin-deficient mutant. Planta 171:525–531

Grover A, Sahi C, Sanan N, Grover A (1999) Taming abiotic stresses in plants through genetic engineering: current strategies and perspective. Plant Sci 143:101–111

Grunberg K, Fernandez-Muñoz R, Cuartero J (1995) Growth, flowering, and quality and quantity of pollen of tomato plants grwon under salline conditions. Acta Hort 412:484–489

Guerrier G (1996) Fluxes of Na+, K+ and Cl-, and osmotic adjustment in *Lycopersicon pimpinellifolium* and *L. esculentum* during short- and long-term exposures to NaCl. Physio Plant 97:583–591

Haigh AH, Barlow EWR (1987) Water relations of tomato seed germination. Austral J Plant Physiol 14:485–492

Hegarty TW (1978) The physiology of seed hydration and dehydration, and the relation between water stress and the control of germination: A review. Plant, Cell Environ 1:101–119

Hsiao TC (1973) Plant responses to water stress. Annu Rev Plant Physiol 24:519–570.

Hsiao TC, Bradford KJ (1983) Physiological consequences of cellualar water deficits. In: Taylor HM, Jordan WR, Sinclair TR (eds) Limitations to efficient water used in crop production. American Society of Agronomy, Madison, Wis., pp 227–

Hsieh T-H, Lee J-T, Charng Y-Y, Chan M-T (2002) Tomato plants ectopically expressing Arabidopsis CBF1 show enhanced resistance to water deficit stress. Plant Physiol 130:618–626

Johnson DW, Smith SE, Dobrenz AK (1992) Genetic and phenotypic relationships in response to NaCl at different developmental stages in alfalfa. Theor Appl Genet 83:833–838

Johnson WC, Jackson LE, Ochoa O, Wijik Rv, Peleman J, Clair DAS, Michelmore RW (2000) Lettuce, a shallow-rooted crop, and *Lactuca serriola*, its wild progenitor, differ at QTL determining root architecture and deep soil water exploitation. Theor Appl Genet 101:1066–1073

Jones RA (1986a) High salt-tolerance potential in *Lycopersicon* species during germination. Euphytica 35:576–582

Jones RA (1986b) The development of salt-tolerant tomatoes: breeding strategies. Acta Hort 190:101–114

Jones RA, Hashim M, El-Beltagy AS (1988) Developmental responsiveness of salt-tolerant and salt-sensitive genotypes of *Lycopersicon*. In: Whitehead E, Hutchison F, Timmeman B, Varazy R (eds) Arid Lands: Today and Tomorrow. Westview Press, Boulder, pp 765–772

Jones RA, Qualset CO (1984) Breeding crops for environmental stress tolerance. In: Collins GB, Petolino JF (eds) Application of Genetic Engineering to Crop Improvement. Nijihoff/Junk, The Hague, pp 305–340

Kahn TL, Fender SE, Bray EA, O'Connell MA (1993) Characterization of Expression of Drought- and Abscisic Acid-Regulated Tomato Genes in the Drought-Resistant Species *Lycopersicon Pennellii*. Plant Physiol 103:597–605

Kalloo G (1991) Breeding for environmental resistance in tomato. In: Kalloo G (ed) Genetic Improvement of Tomato. Springer-Verlag, Berlin Heidelberg, Germany, pp 153–165

Kasuga M, Miura S, Shinozaki K, Yamaguchi-Shinozaki K (2004) A combination of the arabidopsis *DREB1A* gene and stress-inducible *rd29A* promoter improved drought- and low-temperature stress tolerance in tobacco by gene transfer. Plant Cell Physiol 45:346–350

Kaufman MR (1969) Effects of water potential on germination of lettuce, sunflower, and citrus seeds. Can J Bot 47:1761–1764

Kramer PJ (1980) Water Relations of Plants. Academic Press, New York

Kramer PJ (1983) Water Relations of Plants. Academic Press, New York

Lee J-T, Prasad V, Yang P-T, Wu J-F, Ho T-HD, Charng Y-Y, Chan M-T (2003) Expression of Arabidopsis CBF1 regulated by an ABA/stress inducible promoter in transgenic tomato confers stress tolerance without affecting yield. Plant, Cell Environ 26:1181–1190

Lilius G, Holmberg N, Bulow L (1996) Enhanced NaCl stress tolerance in trangenic tobacco expressing bacterial choline dehydrogenase. Bio/technology 14:177–180

Liptay A, Schopfer P (1983) Effect of water stress, seed coat restraint, and abscisic acid upon different germination capabilities of two tomato lines at low temperature. Plant Physiol 73:935–938

Ludlow MM, Muchow RC (1990) A critical evaluation of traits for improveing crop yields in water-limited environments. Adv Agron 43:107–153

Lutfor-Rahman SM (1998) Eco-physiological study on tomato drought tolerance. Division of Environmental Science and Technology. Kyoto University, Kyoto, Japan, p 80

Lyon CB (1941) Responses of two species of tomatoes and the F_1 generation to sodium sulphate in the nutrient medium. Bot Gaz 103:107–122

Maas EV (1986) Salt tolerance of plants. Appl Agric Res 1:12–26

Maas EV (1990) Crop salt tolerance. In: Tanji KK (ed) Agricultural salinity assessment and management. ASCE Mannuals and Reoprts on Engineering No. 71, New York, pp 262–304

Mano Y, Takeda K (1997) Mapping quantitative trait loci for salt tolerance at germination and the seedling stage in barley (*Hordeum vulgare* L.). Euphytica 94:263–272

Martin B, Nienhuis J, King G (1989) Restriction fragment length polymorphisms associated with water use efficiency in tomato. Science 243:1725–1728

Martin B, Tauer CG, Lin RK (1999) Carbon isotope discrimination as a tool to improve water-use efficiency in tomato. Crop Sci 39:1775–1783

Martin B, Thorstenson YR (1988) Stabel carbon isotope composition (delta ^{13}C), water use efficiency and biomass productivity of *Lycopersicon esculentum*, *Lycopersicon pennellii*, and the F_1 hybrid. Plant Physiol 88:213–217

McCormick S, Niedermeyer J, Fry J, Barnason A, Worsch R, Fraley R (1986) Leaf disk transformation of cultivated tomato (*L. esculentum*) using *Agrobacterium tumifaciens*. Plant Cell Rep 5:81–84

Miller JC, Tanksley SD (1990) RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon*. Theor Appl Genet 80:437–448

Mitchell JH, Siamhan D, Wamala MH, Risimeri JB, Chinyamakobvu E, Henderson SA, Fukai S (1998) The use of seedling leaf death score for evaluation of drought resistance of rice. Field Crops Res 55:129–139

Monforte AJ, Asins MJ, Carbonell EA (1996) Salt tolerance in *Lycopersicon* species. IV. Efficiency of marker-assisted selection for salt tolerance improvement. Theor Appl Genet 93:765–772

Monforte AJ, Asins MJ, Carbonell EA (1997) Salt tolerance in *Lycopersicon* species. V. Does genetic variability at quantitative trait loci affect their analysis? Theor Appl Genet 95:284–293

Monforte AJ, Asins MJ, Carbonell EA (1999) Salt tolerance in *Lycopersicon* spp. VII. Pleiotropic action of genes controlling earliness on fruit yield. Theor Appl Genet 98:593–601

Na JK (2005) Genetic approaches to improve drought tolerance
of tomato and tobacco. Horticulture and Crop Science. The Ohio State University, Wooster, p 119

Nguyen HT, Babu RC, Blum A (1997) Breeding for drought resistance in rice: Physiology and molecular genetics considerations. Crop Sci 37:1426–1434

Norlyn JD, Epstein E (1984) Variablility in salt tolrance of four Triticale line at germination and emergence. Crop science 24:1090–1092

Oh S-J, Song SI, Kim YS, Jang H-J, Kim S-Y, Kim M, Kim Y-K, Nahm BH, Kim J-K (2005) Arabidopsis CBF3/DREB1A and ABF3 in transgenic rice increased tolerance to abiotic stress without stunting growth. Plant Physiol 138:341–351

Pearen JR, Pahl MD, Wolynetz MS, Hermesh R (1997) Association of salt tolerance at seedling emergence with adult plant performance in slender wheatgrass. Can J Plant Sci 77:81–89

Perez-Alfocea F, Estan MT, Caro M, Bolarin MC (1993a) Response of tomato cultivars to salinity. Plant and Soil 150:203–211

Perez-Alfocea F, Estan MT, Caro M, Guerrier g (1993b) Osmotic adjustment in *Lycopersicon esculentum* and *L. pennellii* under NaCl and polyethylene 6000 iso-osmotic stresses. Physiologia Plantarum 87:493–498

Perez-Alfocea F, Guerrier G, Estan MT, Bolarin MC (1994) Comparative salt responses at cell and whole-plant levels of cultivated and wild tomato and their hybrid. J Hort Sci 69:639–644

Phills BR, Peck NH, McDonald GE, Robinson RW (1979) Differential responses of *Lycopersicon* and *Solanum* species to salinity. J Am Soc Hortic Sci 104:349–352

Pillay I, Beyl C (1990) Early responses of drought-resistant and -susceptible tomato plants subjected to water stress. J Plant Growth Regul 9:213–219

Plant AL, Cohen A, Moses MS, Bray EA (1991) Nucleotide sequence and spatial expression pattern of drought- and ABA-induced gene for tomato. Plant physiol 97:900–906

Quesada V, Garcia-Martinez S, Piqueras P, Ponce MR, Micol JL (2002) Genetic architecture of NaCl tolerance in Arabidopsis. Plant Physiol 130:951–963

Rana MK, Kalloo G (1989) Morphological attributes associated with the adaptation under water deficit conditions in tomato (*L. esculentum* Mill.).12th Eucarpia Congress 1989, Vortrage Pflanzenzucht, pp 23–27

Rana MK, Kalloo G (1990) Evaluation of tomato genotypes under drought conditions (Abstr.).23rd International Horticultre Congress, Firenze, Italy

Rathinasabapathi B (2000) Metabolic engineering for stres tolerance: Installing osmoprotectant synthesis pathways. Anna Bot 86:709–716

Redmann RE (1974) Osmotic and specific ion effects on the germination of alfalfa. Can J Bot 52:803–808

Ribaut JM, Jiang C, Gonzalez-de-Leon D, Edmeades GO, Hoisington DA (1997) Identification of quantitative trait loci under drought conditions in tropical maize. 2. Yield components and marker-assisted selection strategies. Theor Appl Genet 94:887–896

Richards MA, Phills BR (1979) Evaluation of Lycopersicon species for drought tolerance (Abstr.). HortScience 14:121

Richards RA (1983) Should selection for yield in saline regions be made on saline or non-saline soils? Euphytica 32:431–438

Richards RA (1996) Defining selection criteria to improve yield under drought. Plant Growth Regul 20:157–166

Richards RA, Dennett CW (1980) Variation in salt concentration in a wheat field. Soil and Water 44:8–9

Rick CM (1973) Potential genetic resources in tomato species: clues from observation in native habitats. In: Srb AM (ed) Genes, Enzymes, and Populations. Plenum Press, New York, USA, pp 255–269

Rick CM (1976a) Natural variability in wild species of *Lycopersicon* and its bearing on tomato breeding. Genet Agraria 30:249–259

Rick CM (1976b) Tomato, *Lycopersicon esculentum* (Solanaceae). In: Simmonds NW (ed) Evolution of Crop Plants. Longman, London, UK, pp 268–273

Rick CM (1978) The Tomato. Sci Amer 23:76–87

Rick CM (1979a) Biosystematic studies in *Lycopersicon* and closely related species of *Solanum*. In: Hawkes JC, Lester RN, Skelding AD (eds) The Biology and Taxnomy of the Solanaceae. Academic Press, New York, USA, pp 667–678

Rick CM (1979b) Potential improvement of tomatoes by controlled introgression of genes from wild speies. Proc Conf Broadening Genetic Base of Crops. Pudoc, Wageningen, pp 167–173

Rick CM (1980) Tomato. Hybridization of Crop Plants. Am. Soc. Agron./Crop Sci. Soc. Am., Madison, WI, USA, pp 669–680

Rick CM (1982) The potential of exotic germplasm for tomato improvement. In: Vasil IK, Scowcroft WR, Frey KJ (eds) Plant Improvement and Somatic Cell Genetics. Academic Press, New York, pp 1–28

Rick CM, DeVerna JW, Chetelat RT, Stevens MA (1987) Potential contributions of wild crosses to improvement of processing tomatoes. Acta Hort 200:45–55

Rick CM, Fobes JF (1975) Allozyme variation in the cultivated tomato and closely related species. Bul Torrey Bot Club 102:376–384

Romero-Aranda R, Soria T, Cuartero J (2001) Tomato plant-water uptake and plant-water relationships under saline growth conditions. Plant Sci 160:265–272

Rontein D, Basset G, Hanson AD (2002) Metabolic engineering of osmoprotectant accumulation in plants. Metabolic Engin 4:49–56

Ross R, Lott N (2000) A climatology of recent extreme weather and climate events. U.S. Department of Commerce, Technical Report 2000–02, NOAA/NESDIS, National Climatic Data Center, Asheville, NC

Rush DW, Epstein E (1976) Genotypic responses to salinity: differences between salt-sensitive and salt-tolerant genotypes of the tomato. Plant Physiol 57:162–166

Rush DW, Epstein E (1981a) Breeding and selection for salt tolerance by the incorporation of wild germplasm into a domestic tomato. J Am Soc Hort Sci 106:699–704

Rush DW, Epstein E (1981b) Comparative studies on the sodium, potassium, and chloride relations of a wild halophytic and domestic salt-sensitive tomato species. Plant Physiol 68:1308–1313

Sacher RF, Staples RC, Robinson RW (1983) Ion regulation and response of tomato to sodium chloride: A homeostatic system. J Amer Soc Hort Sci 108:566–569

Santa-Cruz A, Perez-Alfocea F, Caro M, Acosta M (1998) Polyamines as short-term salt tolerance traits in tomato. Plant Sci 138:9–16

Saranga Y, Cahaner A, Zamir D, Marani A, Rudich J (1992) Breeding tomatoes for salt tolerance: Inheritance of salt tolerance and related traits in interspecific populations. Theor Appl Genet 84:390–396

Saranga Y, Zamir D, Marani A, Rudich J (1991) Breeding tomatoes for salt tolerance: Field evaluation of *Lycopersicon* germplasm for yield and dry matter production. J Am Soc Hort Sci 116:1067–1071

Saranga Y, Zamir D, Marani A, Rudich J (1993) Breeding tomatoes for salt tolerance: variation in ion concentration associated with response to salinity. J Am Soc Hort Sci 118:405–408

Sarg SMH, Wyn-Jones RG, Omar FA (1993) Salt tolerance in the Edkawy tomato. In: Lieh H, Al-Masoom A (eds) Towards the rational use of high salinity tolerant plants. Kluwer Academin Publishers, The Netherlands, pp 177–184

Schonfeld MA, Johnson RC, Carver BD, Mornhinweg DW (1988) Water relations in wheat as drought resistance indicators. Crop Sci 28:526–531

Seki M, Kamei A, Yamaguchi-Shinozakiz K, Shinozaki K (2003) Molecular responses to drought, salinity and frost: Common and different paths for plant protection. Curr Opin Biotech 14:194–199

Serrano R, Culiañz-Macia FA, Moreno V (1999) Genetic engineering of salt and drought tolerance with yeast regulatory genes. Scientia Hort 78:261–269

Shannon MC, Gronwald JW, Tal M (1987) Effects of salinity on growth and accumulation of organic and inorganic ions in cultivated and wild tomato species. J Am Soc Hort Sci 112:416–423

Shen B, Jensen RG, Bohnert JJ (1997) Mannitol protects against oxidation by hydroxul radicals. Plant Physiol 115:527–532

Shou H, Bordallo P, Wang K (2004) Expression of the *Nicotiana* protein kinase (NPK1) enhanced drought tolerance in transgenic maize. Exp Bot 55:1013–1019

Stoner AK (1972) Merit, Red Rock and Potomac-tomato varieties adapted to mechanical harvesting. USDA Prod. Res. Rep.

Subbiah P (2001) Genetic Investigation of Abiotic Stress Tolerance in Lycopersicon Species.Genetics. The Pennsylvania State University, University Park, p 104

Subudhi PK, Rosenow DT, Nguyen HT (2000) Quantitative trait loci for the stay green trait in sorghum (*Sorghum bicolor* L. Moench): consistency across genetic backgrounds and environments. Theor Appl Genet 101:733–741

Tal M (1971) Salt tolerance in the wild relatives of the cultivated tomato: Responses of *Lycopersicon esculentum*, *L. peruvianum*, and *L. esculentum minor* to sodium chloride solution. Aust J Agric Res 22:631–638

Tal M (1985) Genetics of salt tolerance in higher plants: Theoretical and practical considerations. Plant and Soil 89:199–226

Tal M (1997) Wild germplasm for salt tolerance in plants. In: Jaiwal PK, Singh RP, Gulati A (eds) Strategies for improving salt tolerance in higher plants. Science Publishers, Inc., U.S.A., pp 291–320

Tal M, Gavish U (1973) Salt tolerance in the wild relatives of the cultivated tomato: Water balance and abscisic acid in *Lycopersicon esculentum* and *L. peruvianum* under low and high salinity. Aust J Agric Res 24:353–361

Tal M, Katz A, Heikin H, Dehan K (1979) Salt tolerance in the wild relatives of the cultivated tomato: proline accumulation in *Lycopersicon esculentum* Mill., *L. peruvianum* Mill., and *Solanum pennellii* Cor. treated with NaCl and polyethylene glycol. New Phytol 82:349–355

Tal M, Shannon MC (1983) Salt tolerance in the wild relatives of the cultivated tomato: Responses of *Lycopersicon esculentum*, *L. cheesmanii*, *L. peruvianum*, *Solanum pennellii* and F_1 hybrids to high salinity. Aust J Plant Physiol 10:109–117

Tanaka Y, Hibino T, Hayashi Y, Tanaka A, Kishitani S, Takabe T, Yokota S, Takabe T (1999) Salt tolerance of trangenci rice overexpressing yeast mitochondrial Mn-SOD in chloroplasts. Plant Science 148:131–138

Tanji KK (1990) Nature and extent of agricultural salinity. In: Tangi KK (ed) Agricultural Salinity Assessment and Management. Am. Soc. Civil Engineers, New York, pp 1–13

Thomas JC, Sepahi M, Arndall B, Bohnert HJ (1995) Enhancement of seed germination in high salinity by engineering mannitol expression in *Arabidopsis thaliana*. Plant Cell Envr 18:801–806

Ungar IA (1978) Halophyte seed germination. The Bot Rev 44:233–264

USDA (2005) Agricultural statistics 2005. United State Department of Agtriculture, National Agricultural Staticstics Service

van Ieperen W (1996) Effects of different day and night salinity levels on vegetative growth, yield and quality of tomato. J Hort Sci 71:99–111

Wang W-X, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218:1–14

Warnock SJ (1988) A review of taxonomy and phylogeny of the genus *Lycopersicon*. HortScience 23:669–673

Warren GF (1998) Spectacular increases in crop yields in the twentieth century. Weed Technol 12:752–760

Wudiri BB, Henderson DW (1985) Effects of water stress on flowering and fruit set in processing tomatoes. Sci Hortic 27:189–198

Xue Z-Y, Zhi D-Y, Xue G-P, Zhang H, Zhao Y-X, Xia G-M (2004) Enhanced salt tolerance of transgenic wheat (*Triticum aestivum* L.) expressing a vacuolar Na+/H+ antiporter gene with improved grain yields in saline soils in the field and a reduced level of leaf Na+. Plant Sci 167:849–859

Yamaguchi T, Blumwald E (2005) Developing salt-tolerant crop plants: Challenges and opportunities. Trends Plant Sci 10:615–620

Yeo AR, Flowers TJ (1990) Screening of rice (*Oryza sativa* L.) genotypes for physiological characters contributing to salinity resistance, and their relationship to overall performance. Theor Appl Genet 79:377–384

Yin XY, Yang A-F, Zhang K-W, Zhang J-R (2004) Production and analysis oftransgenic maize with improved salt tolerance by the introduction of *AtNHZ1* gene. Acta Bot Sin:854–861

Younis AF, Hatata MA (1971) Studies on the effects of certain salts on germination, on growth of root, and on metabolism. I. Effects of chlorides and sulphates of sodium, potassium, and magnesium on germination of wheat grains. Plant and Soil 13:183–200

Yu TT (1972) The genetics and physiology of water usage in *Solanum pennellii* Corr. and its hybrids with *Lycopersicon esculentum* Mill. University of Cal., Davis

Zhang HX, Blumwald E (2001) Transgenic salt-tolerant tomato plants accumulate salt in foliage but not in fruit. Nature biotechnology 19:765–768

Zhang HX, Hodson JN, Williams JP, Blumwald E (2001a) Engineering salt-tolerant *Brassica* plants: Characterization of yield and seed oil quality in transgenic plants with increased vacuolar sodium accumulation. Proc Natl Acad Sci USA 98:12832–12836

Zhang J, Zheng HG, Aarti A, Pantuwan G, Nguyen TT, Tripathy JN, Sarial AK, Robin S, Babu RC, Nguyen BD, Sarkarung S, Blum A, Nguyen HT (2001b) Locating genomic regions associated with components of drought resistance in rice: comparative mapping within and a cross species. Theor Appl Genet 103:19–29

Zhang JZ, Creelman RA, Zhu J-K (2004) From laboratory to field. Using information from Arabidopsis to engineer salt, cold, and drought tolerance in crops. Plant Physiol 135:615–621

Zhu JK, Hasegawa PM, Bressan RA (1997) Molecular aspects of osmotic stress in plants. Crit Rev Plant Sci 16:253–277