



# Salinity stress in cotton: effects, mechanism of tolerance and its management strategies

Iram Sharif<sup>1</sup> · Saba Aleem<sup>2</sup> · Jehanzeb Farooq<sup>1</sup> · Muhammad Rizwan<sup>1</sup> ·  
Abia Younas<sup>1</sup> · Ghulam Sarwar<sup>1</sup> · Shahid Munir Chohan<sup>1</sup>

Received: 26 December 2018 / Revised: 15 April 2019 / Accepted: 13 May 2019 / Published online: 20 June 2019  
© Prof. H.S. Srivastava Foundation for Science and Society 2019

**Abstract** Cotton is classified as moderately salt tolerant crop with salinity threshold level of  $7.7 \text{ dS m}^{-1}$ . Salinity is a serious threat for cotton growth, yield and fiber quality. The sensitivity to salt stress depends upon growth stage and type of salt. Understanding of cotton response to salinity, its resistance mechanism and looking into management techniques may assist in formulating strategies to improve cotton performance under saline condition. The studies have showed that germination, emergence and seedling stages are more sensitive to salinity stress as compared to later stages. Salt stress results in delayed flowering, less fruiting positions, fruit shedding and reduced boll weight which ultimately affect seed cotton yield. Depressed activities of metabolic enzymes viz: acidic invertase, alkaline invertase and sucrose phosphate synthase lead to fiber quality deterioration in salinity. Excessive sodium exclusion or its compartmentation is the main adaptive mechanism in cotton under salt stress. Up regulation of enzymatic and non-enzymatic antioxidants genes offer important adaptive potential to develop salt tolerant cotton varieties. Seed priming is also an effective approach for improving cotton germination in saline soils. Intra and inter variation in cotton germplasm could be used to develop salt tolerant varieties with the aid of marker assisted selection. Furthermore, transgenic approach could be the promising option for enhancing cotton production under saline condition. It is suggested that future research may be carried out with the

combination of conventional and advance molecular technology to develop salt tolerant cultivars.

**Keywords** Cotton · Functional genomic · Ion homeostasis · Salinity · Seed priming · Germination

## Introduction

Cotton is one of the most important natural fiber crops and used as edible oil and biofuel. It faces several biotic and abiotic stresses during its lifespan, among which salinity has become one of the major threats for sustainable cotton production across the world. Saline soils are defined in term of electrical conductance of saturated paste extract with soils having electrical conductivity of its saturation extract ( $EC_e$ ) higher than  $4 \text{ dS m}^{-1}$  at  $25 \text{ }^\circ\text{C}$  (Allison and Richards 1954). Cotton is moderately salt tolerant crop with salinity threshold level of  $7.7 \text{ dS m}^{-1}$  (Zhang et al. 2013). Many other crops vary in their ability to tolerate salinity levels (Table 1). Salt stress disturbs the osmotic and ionic homeostasis at cellular level, inhibits photosynthesis, and reduces the cellular energy and results in redox imbalance. Consequently, inhibited photosynthesis damage the cellular metabolism which leads to abnormal plant growth (Zhang et al. 2016).

It is estimated that approximately 45 million hectares of irrigated area is salt affected and causes a loss of US \$27.3 billion per year (Anschütz et al. 2014). Estimated 20% of the worldwide cultivated land and 33% of the irrigated agricultural area are salt affected and this area is increasing at the rate 10 percent annually. It is predicted that more than 50% of arable land will be salt effected by 2050 (Jamil et al. 2011). Improper management practices, application of substandard irrigation water and non-availability of

✉ Iram Sharif  
iramsharif695@yahoo.com

<sup>1</sup> Cotton Research Station, AARI, Faisalabad, Pakistan

<sup>2</sup> Vegetable Research Institute, AARI, Faisalabad, Pakistan

**Table 1** An overview of important crops regarding their salt tolerance ability

Crop	Threshold level of EC (dS m <sup>-1</sup> )	Status of crop	Sensitive stages	Yield loss due to salt stress (%)	References
Cotton	7.7	Tolerant	Germination, Emergence till formation of first reproductive branches	50–90	Khorsandi and Anagholi (2009) and Ahmad et al. (2002)
Rice	2	Moderately Sensitive	Tillering, panicle forming, heading and grain formation	30–35	Joseph and Mohanan (2013)
Wheat	6	Moderately tolerant	Booting and grain filling stage	13.4	Mojid et al. (2013)
Maize	1.3	Moderately sensitive	Earlier vegetative growth stages	16–22	Katerji et al. (2000) and Sharif et al. (1999)
Sugarcane	1.7	Moderately sensitive	Vegetative growth and sucrose formation	10–100	Simoes et al. (2016) and Ashraf et al. (2007)
Sorghum	2.8	Moderately sensitive	Emergence, blooming and soft dough stages throughout the growing season	50	Kafi et al. (2018)
Onion	1.21	Sensitive	Seedling, vegetative growth, bulb size and bulb diameter	50	Sta-Baba et al. (2010)

proper drainage system are the major causes of salinity and waterlogging problems in Pakistan and India (Hossain 2010). To combat this stress situation, understanding of the response of crops toward salinity stress and identification of genotypes that have the ability to tolerate stress is necessary to strengthen the breeding program of each crop. This review highlights the impact of salinity on cotton growth and development, plant response to salt stress with activation of defense mechanism, exploring salt responsive genes and the combination of best management strategies to improve the cotton crop efficiency.

### Global status of salt stress

Globally, salinity is the serious problem, and more than half of countries are facing this problem with varying degree of affected area. It typically occurs in arid and semiarid regions of the world, particularly in low lying soils via deposition of free salts (Saddiqe et al. 2016). While classifying the world regions into salt affected soil, it is found that Asia, the Pacific and Australia are the highly salt affected region. Approximately 6% of the total land in Asia, the Pacific and Australia zone is facing salinity problem (Arora 2017). Being located in arid to semiarid region, salinity is also a big concern of Pakistan. It was reported that out of 22 million hectares of agriculture land in Pakistan, 6.28 million hectares are salt affected (Alam et al. 2000). About 60.5% salt affected soil in Pakistan is saline sodic while remaining 39.5% is facing salinity (Ashraf and Ahmad 2000b). Every year, 40,000 ha are lost due to salt stress causing a loss of 3 billion US \$ on annual base (Ansari et al. 2007). This problem is more prevalent in

dried areas which receive less rainfall with more evapotranspiration rate.

### Effect of salinity stress on cotton growth

To deal with saline soils, it is necessary to understand the effects of salt stress on different growth stages of cotton (Table 2).

#### Germination

Cotton germination, emergence and young seedling stage are more prone to salt stress than other stages (Ahmad et al. 2002). Wang et al. (2011) reported that seedling at germination stage is more sensitive to salt stress than seedling at juvenile stage. In cotton, drastic reduction in germination percentage was observed beyond 10 dS m<sup>-1</sup>. In response to salinity stress, germination and emergence stages are also delayed in cotton (Khorsandi and Anagholi 2009; Ma et al. 2011). At salinity stress of 15–20 dS m<sup>-1</sup>, plant emergence was delayed up to 4–5 days as compared to normal plant. Poor germination leads to reduction in plant population that ultimately resulted in severe decrease in cotton yield (Saqib et al. 2002). The germination potential, germination rate, fresh mass, and vigor index could be utilized to evaluate salt tolerance at germination stage (Guo-Wei et al. 2011).

#### Root growth

Salinity usually reduces the root growth due to inhibition of root length and reduction in number of secondary roots (Silberbush and Ben-Asher 1987). Leidi (1994) reported

**Table 2** Summarized findings of salt stress effects during different growth stages of cotton

Growth stage	Possible reason	Effect on growth	References
Germination	Less and delayed germination due to reduced germination potential, fresh mass and vigor index	Negative	Ahmad et al. (2002) and Guo-Wei et al. (2011)
Emergence	Delayed emergence leads to non-availability of nutrients. Less plant vigor which results into poor crop establishment	Negative	Ahmad et al. (2002)
Seedling stage	Reduction in plant height, leaf expansion, root vigor, root dry weight, shoot dry weight and net photosynthetic rate	Negative	Ahmad et al. (2002) and Guo-Wei et al. (2011)
Root growth	Reduction in root length and number of secondary roots, less fresh and dry weight of the roots	Negative	Shaheen et al. (2012) and Silberbush and Ben-Asher (1987)
Flowering and Boll development stage	Delayed onset of flowering, less fruit bearing position, fruit shedding, reduced photosynthetic rate, sucrose transformation rate, boll weight, boll size	Negative	Bernstein and Hayward (1958), Longenecker (1974), Peng et al. (2016a) and Rathert (1983)
Fiber length	Reduced sucrose contents, cellulose contents, sucrose transformation rate and reduced activity of metabolic enzymes (alkaline invertase and SPS)	Negative	Longenecker (1974) and Peng et al. (2016a)
Fiber strength			
Fiber maturity			
Fiber fineness		Positive	Peng et al. (2016b)

that higher concentration inhibited the primary root length, however the length of secondary roots was also retarded at mild salt stress. Plant growth relies on ionic influx in the roots along with their translocation toward shoot. Relatively lower inhibition of root growth than shoot may be attributed to lesser retention of sodium ions in the roots. With the increase in the salinity, root growth reduced significantly in different soils but the suppression in root growth, fresh and dry weight was maximum in clay, loam and intermediate soils while minimum effects were observed in sandy soil (Soliman et al. 1980).

### Shoot growth

Although cotton is classified as relatively salt tolerant crop, but higher salt concentration affects the vegetative growth negatively. Salt stress reduces shoot/root ratio and shoot growth is more sensitive to salinity than roots (Khan et al. 1995). However, some researchers reported that low intensity of salt stress increased the shoot growth. This may be attributed to sparing effect of nutrient or the presence of micronutrients in the form of impurities in the saline growth medium (Kent and Läuchli 1985). Studies carried out at seedling, six leaf, pre flowering, flowering and boll development stages under salt stress reported that six leaf stage was the most sensitive one (Khan et al. 1998a).

### Boll development and yield

Number of bolls and boll size are the major yield contributing parameters. With the increase in the salinity level,

cotton yield decreased accordingly due to reduction in number of bolls and boll weight. Decline in mature bolls is due to reduction in fruit bearing position, delayed flowering, relative increased shedding of flowers and bolls under salt stress (Anagholi et al. 2005). The possible reason of delayed flowering may be the negative effects of salt stress on vegetative growth which ultimately delays the onset of flowering (Bernstein and Hayward 1958). In cotton, 60–87% synthesized sucrose is transported from Subtending Leaf of Cotton Boll (LSCB) to developing bolls and it plays prominent role in cotton yield. Under saline condition, sucrose accumulation in LSCB is not affected but its efficient transportation towards developing bolls is retarded that results in reduced boll weight (Peng et al. 2016a). Cotton yield was reduced by 50% at 17.0 dS m<sup>-1</sup> (Maas and Hoffman 1977) however, moderate level of salinity attributed no adverse effect on growth while with the increase in the salinity, premature leaf senescence and shedding occurred (Rathert 1983). Irrigation of cotton plants at budding stage with highly saline water resulted in 90% yield reduction (El Saidi and Hegazy 1980).

### Fiber quality

Fiber quality is an inherited trait but it is also affected by the environment. Salinity stress reduced the fiber length, strength and maturity while fiber fineness showed increasing trend. With the increase in the sodium ions percentage, fiber length, strength and micronaire values were reduced significantly (Longenecker 1974). Increased electrical conductivity (EC) likely affects the fiber maturity

due to its impact on photosynthesis process, cellulose deposition and sugar transport. Lesser cellulose deposition results in unavoidable decline in the cross sectional area and produces less mature fiber (Yfoulis and Fasoulas 1973). Fiber quality mainly depends on cellulose deposition and sucrose metabolism plays key role in cellulose synthesis (Fernandes et al. 2004). Mature fibers contain more than 85% cellulose, its synthesis and accumulation occur during fiber thickening and its deposition begins after fiber elongation due to increase in cellulose synthesis. With the increase in the salinity level, cellulose contents and sucrose transformation rate were decreased significantly in salt sensitive varieties which results in fiber quality deterioration. Under saline condition sucrose is available, however, it is not efficiently converted into cellulose due to suppressed activities of metabolic enzymes acidic invertase, alkaline invertase and sucrose phosphate synthase (Peng et al. 2016b).

## Physiological response to salinity

### Photosynthesis

Salinity stress results in reduced rate of photosynthesis and the reason behind this is disruption in photosynthetic apparatus and activities. Increased NaCl level in soil resulted into osmotic stress which limits cell expansion rate and reduces stomatal aperture size, affecting the photosynthetic activity. Reduction in leaf area is the first detectable effect of salt stress in plants. Reduced leaf surface area due to restricted cell extensibility is more important at initial stage than the less photosynthetic rate per unit area (Shabala and Lew 2002). Reduction in photosynthetic activities is also attributed to least Ribulose biphosphate (RuBP) carboxylase efficiency under limited supply of RuBP, PSII sensitivity and decline in regeneration capacity of RuBP (Seemann and Sharkey 1986). It is supposed that salt stress might interfere with biochemistry of photosynthesis by disorientation of chloroplast lamellar system and chloroplast integrity loss resulting in reducing photosystem activity. The impact of salt stress on photosynthetic enzymes could be secondary in nature mediated by the lesser CO<sub>2</sub> pressure in the leaves due to stomatal closure.

Meng et al. (2011) reported that decrease in photosynthesis is associated with reduction in chlorophyll contents and alteration in ultra-structure of chlorophyll. Significant reduction in chlorophyll contents (a and b) was observed in cotton cultivars with the increase in salinity level (Zhang et al. 2014). This reduction may be due to suppression of specific enzymes associated with chlorophyll synthesis (Lee et al. 2013). Therefore, among physiological

parameters, chlorophyll contents could be regarded as a good indicator for selection of salt tolerant varieties.

Carotenoids are another key pigment of photosynthetic machinery that are also involved in harvesting light energy during the process of photosynthesis. Decrease in the expression of carotenoids biosynthetic genes when plants are under salinity stress is highly associated with hampering photosynthesis rate which ultimately reduces the yield (Shah et al. 2017). Earlier studies also reported a significant reduction in carotenoids contents in cotton genotypes while increasing salt stress (Zhang et al. 2014). Rafique et al. (2003) reported that carotenoids contents degradation is slower as compared to chlorophyll in salinity stress. At different salinity levels, increase in carotenoids, anthocyanins and flavones contents was recorded while at the same time other photosynthetic pigments i.e. chlorophyll a and b were drastically decreased.

### Inorganic ions

Under salt stress, changes in the concentration of inorganic ions have been reported by many researchers. Different responses have been observed from immense increase in Na<sup>+</sup> and Cl<sup>-</sup> ions with reduction in Mg<sup>2+</sup>, K<sup>+</sup> and Ca<sup>2+</sup> ions (Jafri and Ahmad 1995; Rathert and Doering 1983). Excessive accumulation of Na<sup>+</sup> ions imparts toxic effects on plant physiological process and also reduces water availability. Pervaiz et al. (2007) documented significant increase in Na<sup>+</sup> and Cl<sup>-</sup> ions concentration in cotton leaves with reduced K<sup>+</sup>/Na<sup>+</sup> ratio. Salt tolerant plants regulates the exclusion of Na<sup>+</sup> ions via roots, while the plants which are unable to maintain Na<sup>+</sup> homeostasis were categorized as susceptible. Some studies reported that rather than Na<sup>+</sup> exclusion, maintenance of optimum ratio of K<sup>+</sup>/Na<sup>+</sup> ions determines the performance of plant under salt stress (Dai et al. 2014; Ding et al. 2010).

In addition to sodium and chloride ions, Mn, Zn and N were also increased under salt stress while S, P and Ca<sup>2+</sup> level remained consistent. However, Fe, K<sup>+</sup>, Cu and Mg<sup>2+</sup> ions were reduced significantly under saline condition (Higbie et al. 2010). Leidi and Saiz (1997) reported higher dry matter, water contents and water potential along with higher deposition of Na<sup>+</sup> ions in the leaves of salt tolerant genotypes than susceptible ones. These findings suggest that tolerance mechanism is linked with higher uptake of Na<sup>+</sup> ions and water contents. Like some halophytes, adaptation via sufficient but controlled ions uptake is similar to effective compartmentation and redistribution of ions and it would increase water uptake capacity and improve growth rate.

Ionic imbalance restricts the nutrients access and transport within plants due to Na<sup>+</sup> and Cl<sup>-</sup> ions competition with other nutrients like NO<sup>3-</sup>, Ca<sup>2+</sup>, and K<sup>+</sup> and

results in reduced concentration of  $Mg^{+2}$ ,  $Ca^{2+}$ ,  $K^+$ , P and N in roots and leaves (Mansour et al. 2005; Zhang et al. 2014). However, several findings have reported stable concentration of S,  $Ca^{2+}$  and  $K^+$  in leaves resulting into lower  $K^+/Ca^{2+}$  or  $K^+/Na^+$  ratios (Abd Ella and Shalaby 1993). Thomas (1980) documented increased concentration of  $Ca^{2+}$  and  $Mg^{+2}$  ions in the leaves. To mitigate the negative effects of salinity on plant productivity, it is necessary to understand these nutritional disorders.

## Tolerance mechanism

### Organic solutes

To overcome the salt stress, accumulation of osmoprotectants e.g. amino acids, sugars, glycine betaine, polyols and polyamines for metabolic adjustment significantly contributes toward salt tolerance. In order to balance the osmotic potential inside the vacuole, organic ions are compartmentalized within vacuole. These organic solutes assist in stabilizing the membranes and protein against denaturing activity of harmful solutes and salts, maintain cell turgor and provide gradient force for water uptake (Naidoo and Naidoo 2001; Rontein et al. 2002).

Glycine betaine is an important organic solute that acts as an osmoprotectants and accumulates in drought, salinity and as well as in extreme temperature stress (Quan et al. 2004). Several researchers reported glycine betaine contribution toward osmotic adjustment in salinity stress (Khan et al. 1998b). Zhang et al. (2009) observed high glycine betaine in response to salinity tolerance in transgenic cotton lines in which Choline monoxygenase (*CAM*) gene that is involved in catalytic pathway for conversion of choline into betaine aldehyde which is further catalyzed by different enzymes into glycine betaine was genetically engineered.

Proline plays important role in stabilizing RUBISCO enzyme and promotes its functionality even in the presence of NaCl. Level of free proline was enhanced in *G. arborum* and *G. hirsutum* after treating with sea water (Ahmad and Abdullah 1982). Meloni et al. (2001) reported 36% increase in proline contents in the roots of treated plants than control, while in the leaves, proline level was enhanced by 121% after treating with NaCl. Golan-Goldhirsh et al. (1990) reported contradictory results in which he found non consistent changes in proline or hydroxyproline contents in cotton against salinity stress. Thus, proline concentration is not enough to meet the osmotic adjustment, however, it could play significant role if confined to cytosol.

## Membrane and transport

In salt stress, regulation of ion flux is necessary to retain low concentration of harmful ions and to acquire essential ions. Under normal situation, high  $K^+/Na^+$  ratio is maintained in the plant cell cytosol with higher  $K^+$  levels and lower  $Na^+$  level (Higinbotham 1973). Under saline condition,  $Na^+/K^+$  ratio and sodium ion concentration is increased in the roots of plant and results in hyperosmotic stress, ionic imbalance and toxicity. The reason behind this ionic imbalance is that under saline condition, hydrated form of  $Na^+$  and  $K^+$  ions become similar and make it difficult for  $K^+$  influx pathway to discriminate between  $Na^+$  and  $K^+$ , resulting in influx of  $Na^+$  from  $K^+$  influx pathway that ultimately causes the  $Na^+$  toxicity in cytoplasm. To maintain  $Na^+/K^+$  ratio, salt tolerant plants reduce the influx of  $Na^+$  from roots, compartmentalized the existing  $Na^+$  present in the cytosol to vacuole and make efflux of  $Na^+$  from root cells (Keisham et al. 2018).

Plant cells utilize primary active transport facility via  $H^+$ -ATPases, channels i.e.  $K^+$  channel (AKT1), co-transporters mediated secondary transport i.e. High affinity  $Na^+$  transporter (HKTs) and High affinity  $K^+$  transporter (HAK5),  $Na^+/H^+$  antiporters i.e.  $Na^+/H^+$  exchangers (NHX) for vacuolar compartmentalization, Salt overly sensitive (SOS) pathway for  $Na^+$  efflux and to keep high  $K^+/Na^+$  ratio in the cytosol (Conde et al. 2011; Zhao et al. 2013). Sustaining high ratios of  $Ca^{2+}/Na^+$  and  $K^+/Na^+$  in response to salt stress is regarded as key selection criteria. In salt tolerant cotton genotypes, high selective absorption of  $K^+$  over  $Na^+$  was kept by the down-regulation of *GhSOS1*, *AKT1* and *HAK-5* and at the same time through up-regulation of *GhHKT1* and *GhNXH1*. This shows that salt tolerance in cotton genotype is highly linked with regulation of  $K^+$  and  $Na^+$  ions by compartmentalization of  $Na^+$  ion into vacuole as compared to  $K^+$  uptake (Wang et al. 2017).

ABC (ATP-binding cassette) transporters carries stress linked secondary metabolites like quinines, terpenoids, alkaloids and polyphenols (Theodoulou 2000) and affects the homeostasis of  $Na^+/K^+$  ions and alleviate the salt stress (Lee et al. 2004). In cotton roots, up-regulation of ABC transporters (gil224130846) suggests its possible role toward salt tolerance. Response of the ABC transporters varies in several types of salinity stresses. Transcriptome analyses carried out during  $Na_2CO_3$ , NaCl, and NaOH stress in cotton reported an up-regulation of five ABC genes (*Gh\_A12G1090*, *Gh\_A10G0583*, *Gh\_A05G1089*, and *Gh\_Sca006272G01*), and ABC2 (*Gh\_A09G1286*) in response to  $Na_2CO_3$  and NaCl stress to transport micro-molecules for ion homeostasis (Zhang et al. 2018). Aquaporin channels proteins which assist in water, gasses and small neutral solutes transportation in the intracellular and



plasma membrane are linked with stress tolerance in plant. Tonoplast intrinsic proteins (TIPs) and plasma membrane intrinsic proteins (PIPs) are the two most abundant sub-families of aquaporin. It was reported that in cotton, expression of both PIPs and TIPs proteins was down regulated to prevent the water loss under saline condition (Li et al. 2015).

### Antioxidants

In plant, increased activity of antioxidants is associated with salt tolerance (Noreen and Ashraf 2009). Salt stress induced the production of Reactive Oxygen Species (ROS) like superoxide, hydroxyl radical and hydrogen peroxide. In normal condition, ROS are neutralized via intracellular antioxidants while under salt stress, excessive accumulation of ROS provoke oxidative stress and severely disturb the normal metabolism, cause protein destruction and mutation in nucleic acid (Czégény et al. 2014).

To alleviate salinity induced oxidative damage, plants carries two types of antioxidant system viz enzymatic and non-enzymatic. Enzymatic antioxidant system includes glutathione peroxidase, superoxide dismutase (SOD), catalase (CAT) and peroxidases (POD) along with enzymes of ascorbate–glutathione peroxidase [glutathione reductase (GR) and ascorbate peroxidase (APX)]. SOD is regarded as major antioxidant enzyme because it regulates  $O_2^{2-}$  and  $H_2O_2$  concentration. APX and CAT revealed efficient  $H_2O_2$  scavenging ability. In the presence of SOD, APX and CAT played vital protective role during scavenging process (Zhang et al. 2014). While non-enzymatic antioxidant system consist of ascorbic acid, tocopherols, carotenoids and glutathione (Ashraf 2009; Foyer and Noctor 2000). In cotton, it was observed that with the rise in NaCl intensity, the activities of SOD were also increased. While POD activity were enhanced up to 53% in resistant cultivar. Increased POD activity enhanced photosynthetic activity which revealed the role of antioxidants defense mechanism to mitigate salt stress (Zhang et al. 2014). Rajguru et al. 1999 linked the salt tolerance during fiber development with the increased activity of enzymatic antioxidant i.e. glutathione reductase, ascorbate peroxidase, superoxide dismutase.

Inhibitor studies depicted that due to de novo transcription of the genes, glutathione reductase and ascorbate oxidase activities were enhanced (Manchandia et al. 1999). These findings suggest the possible role of antioxidation systems especially ascorbate glutathione cycle for salt resistance. Ascorbate/ascorbic acids is another important non-enzymatic antioxidant whose concentration is increased in chloroplast and cytosol during salinity stress and has the ability to protect the photosynthetic machinery. In early cotton growth stages, an increase in ascorbic acid

contents in tolerant genotypes over susceptible ones is reported (Aslam et al. 2013).

## Management strategies of salt stress

### Functional genomics

Among different cultivated cotton species, *G. barbadense* was classified as more salt tolerant (Ahmad et al. 2002) while among wild species of cotton, *Gossypium davidsonii* has salt stress tolerance ability (Zhang et al. 2016). In *G. hirsutum*, D-subgenome is major contributor of salt tolerance (Li et al. 2014). The researchers have focused on molecular factors involved in response to salt stress and attempted to manipulate these genes for the development of salt tolerant genotypes (Table 3).

Considerable variation lies in cotton germplasm and exploring the germplasm may lead to development of salt tolerant cultivars. Transcription factors are regarded as key regulators of genes expression. Many salt responsive genes have been documented in other plants but in cotton, few salt resistant genes have been identified e.g. ZFP (Guo et al. 2009), MKK (Lu et al. 2013), ERF (Johnson et al. 2003), NAC (Meng et al. 2009), DREB (Gao et al. 2009), MPK (Zhang et al. 2011), GhMT3a (Xue et al. 2008) and tonoplast  $Na^+/H^+$  antiporter (Wu et al. 2004). Fan et al. (2015) documented 109 WRKY genes (GarWRKYs) in wild salt tolerant *G. aridum* via transcriptome sequencing data and through RT-PCR analysis confirmed the expression of 27 GarWRKY genes in the roots.

Overexpression of Reactive Oxygen Species (ROS) scavengers like GhMT3a, GhSOD1 and GhCAT1 displayed high tolerance in cotton against salt stress (Luo et al. 2013). A novel gene (*GhNHX1*) has the function of tonoplast,  $Na^+/H^+$  antiporter and regulates the defense response against salt stress. The expression analysis revealed that mRNA level of *GhNHX1* was higher in salt tolerant cultivar than salt sensitive cultivars suggesting its importance toward salt tolerance mechanism (Wu et al. 2004).

### Marker assisted selection

Salt tolerance is a complex quantitative trait that is controlled by many genes each of which have small effect. It is impossible to elucidate its genetic control through a single gene-based studies. Genetic basis of salt tolerance in various plants have been explained by QTL (quantitative trait loci) analyses. Most of the work regarding QTL mapping for salinity tolerance has been published regarding rice crop and SALTOL locus which is linked to QTLs for the uptake of  $Na^+$  and  $K^+$  and  $Na^+/K^+$  ratio maintenance has

**Table 3** Functional genomics of salt responsive genes in cotton

Genes	Functional study	Growth stage (tissue)	Cotton species (cultivar)	References
<i>GhERF2</i>	ERF-encoding gene	Mature plant (Cotyledon, embryo, leaves, roots, stem and flower)	<i>G. hirsutum</i> (Zhongmian 12)	Jin et al. (2010)
<i>GhERF3</i>	ERF-encoding gene	Mature Plant (Stem, roots, flowers and leaves)	<i>G. hirsutum</i> (Zhongmian 12)	Jin et al. (2010)
<i>GhERF6</i>	ERF-encoding gene	Mature plant (Cotyledon, flower, roots, stem and leaves)	<i>G. hirsutum</i> (Zhongmian 12)	Jin et al. (2010)
<i>GhERF38</i>	ERF-encoding gene	Seedling (Cotyledon, hypocotyls, roots and leaves)	<i>G. hirsutum</i> (Coker 312)	Ma et al. (2017)
<i>GhABF2</i>	bZIP-encoding gene	Seedling (leaves, roots, stem)	<i>G. hirsutum</i> (Simian 3)	Liang et al. (2016)
<i>GhAnn1</i>	Annexin gene	Seedling (leaves)	<i>G. hirsutum</i> (7235)	Zhang et al. (2015)
<i>GhNAC1–GhNAC6</i>	Encode NAC domain	–	<i>G. hirsutum</i>	Shah et al. (2013)
<i>GhNAC4, GhNAC6</i>	Encode NAC domain	Seedling (leaves)	<i>G. hirsutum</i> (Jinmian 19)	Meng et al. (2009)
<i>GhMKK1</i>	Mitogen-activated protein kinase kinase	Seedling (cotyledon leaves, roots and stems)	<i>G. hirsutum</i> (Lumian 22)	Lu et al. (2013)
<i>GhWRKY11</i> <i>GhWRKY12</i> <i>GhWRKY13</i> <i>GhWRKY14</i> <i>GhWRKY115</i> <i>GhWRKY20</i> <i>GhWRKY21</i> <i>GhWRKY24</i> <i>GhWRKY30</i> <i>GhWRKY32</i> <i>GhWRKY33</i> <i>GhWRKY34</i>	WRKY transcription factor	Seedlings (roots)	<i>G. hirsutum</i> (Coker 312)	Zhou et al. (2014)
<i>GhWRKY39</i>	WRKY transcription factor	Seedling (leaves, roots and stems)	<i>G. hirsutum</i> (Lumian 22)	Shi et al. (2014b)
<i>GhWRKY39-1</i>	WRKY transcription factor-encoding	Seedling	<i>G. hirsutum</i> (Lumian 22)	Shi et al. (2014a)
<i>GhWRKY41</i>	WRKY transcription factor-encoding	Seedling (leaves, roots, stem)	<i>G. hirsutum</i> (Lumian 22)	Chu et al. (2015)
<i>GhWRKY25</i>	WRKY transcription factor-encoding	Seedlings (leaves, stem, roots)	<i>G. hirsutum</i> (Lumian 22)	Liu et al. (2016)
<i>GhTPS11</i>	Trehalose-6-phosphate synthase (gene)	Seedling (Cotyledon, stem, roots)	<i>G. hirsutum</i> (ZM19)	Wang et al. (2016)
<i>GhDi19-1</i> <i>GhDi19-2</i>	Drought induced protein which is Cys2/His2 zinc-finger proteins	Seedling (Cotyledons, roots)	<i>G. hirsutum</i> (Xuzhou 142 and Coker 312)	Li et al. (2010)
<i>GhMAP3K40</i>	Mitogen-activated protein kinase gene	Seedling (leaves, roots and stem)	<i>G. hirsutum</i> (Lumian 22)	Chen et al. (2015)
<i>GhSOD1</i>	Superoxide dismutase	Mature plant (stems, leaves and ovules)	<i>G. hirsutum</i> (Zhongmiansuo 3)	Luo et al. (2013)
<i>GhAPX1</i> <i>GhCAT1</i>	Ascorbate peroxidase Catalase	Seedling (leaves and roots) Mature plant (leaves and ovules)		
<i>GhNHX1</i>	Tonoplast Na <sup>+</sup> /H <sup>+</sup> antiporter	Seedling (cotyledon, leaves, stem, roots)	<i>G. hirsutum</i> (ZM3)	Wu et al. (2004)
<i>GhDREB</i>	Dehydration responsive element binding protein gene	Seedling (leaves)	<i>G. hirsutum</i> (Simian 3)	Gao et al. (2009)

**Table 3** continued

Genes	Functional study	Growth stage (tissue)	Cotton species (cultivar)	References
GhCCL	Cold-circadian rhythm-RNA binding-like protein	Germination	<i>G. hirsutum</i> (Bikaneri Narma)	Dhandapani et al. (2015)

been mapped (Wang et al. 2012). Marker assisted selection is a promising approach for indirect selection of salt tolerant genotypes. An overview of different molecular markers linked to salinity tolerance is listed in Table 4. Association analysis by using 145 SSRs was conducted to

map 10 salt tolerant traits in cotton, among these 95 SSRs showed significant associations with salt tolerant characters, out of which 41 were linked to seedling stage physiological index, 37 to biochemical index at four seedling stage and 17 to germinative index (Du et al. 2016).

**Table 4** An overview of different markers reported for selection of salt tolerant genotypes in cotton

Marker/gene name	Marker type	Linked trait	Location on chromosome	References
BNL3103	SSR	Dry plant weight (DPW), dry root weight (DRW)	D06	Saeed et al. (2014)
NAU478		Root shoot ratio (RSR), dry root weight (DRW)	D08	
BNL3140		Root shoot ratio (RSR), dry root weight (DRW)	D09	
NAU2679		Shoot length (SL), fresh shoot weight (FSW), fresh plant weight (FPW)	A06	
NAU1008(b)- NAU3608	QTL (qRL-Chr16-1)	Root length (RL)	16	Oluoch et al. (2016)
HAU2866-DPL0573	qRL-Chr22-1		22	
NAU5189-G	SSR	Relative root dry matter (RRDM)	D09	Du et al. (2016)
NAU2161-H		Relative chlorophyll content (RCC)	A03	
NAU2173-C			D02	
NAU483-B		Relative growth rate (RGR)	A03	
NAU2190-C		Relative plant height (RPH)	D02	
NAU7049-B		Relative SOD (RSOD)	A01	
EPIC356/C4	ILP	WARKY DNA binding protein	A12	Cai et al. (2017)
EPIC109/C9 (MPK9)		Mitogen-activated protein kinase	A03	
i28278Gh, i31650Gh, i28055Gh	SNP	Relative survival rate (RSR)	A10	Sun et al. (2018)
i31466Gh, i04513Gh, i38423Gh			D08	
i46598Gh, i47388Gh			D09	
i12146Gh			D10	
i06916Gh			D11	
i46938Gh		Salt tolerance level (STL)	A01	
i04851Gh, i47348Gh			D02	
i46598Gh, i47388Gh			D09	
i12076Gh, i60613 Gb, i42017Gh, i24986Gh, i33471Gh, i20955Gh, i40669Gh, i43909Gh, i22025Gh				
i29606Gh			D10	



By using association analysis, eight SSRs were linked to salt tolerance out of which two were significantly associated with salt tolerance and described phenotypic variations from 7.82 to 6.26% (Zhao et al. Zhao et al. 2016). Proteomic techniques can be used as a tool to identify proteins linked with salt resistance. In a study, iTRAQ identified 58 differentially abundant salt responsive proteins in seedling leaves of cotton. Phosphate-related differentially abundant proteins (DAPs), N-methyltransferase 1, 14-3-3-like protein E and phospho ethanol amine were induced in salt stress. Twenty-nine salt responsive proteins were found genotype-specific and 27.6% and 62.1% of these were associated with defense response and chloroplast respectively (Gong et al. 2017). These findings suggest efficacy of marker assisted selection for identification and development of salt tolerant genotypes.

### Transgenic approaches

Transfer of the desirable genes to get required characters in term of qualitative and quantitative traits is known as transgenic approach. This technology works across the species or even genera, it is quicker than conventional breeding and avoids the transfer of undesirable or the surplus genes. Transgenic approach not only facilitated the identification of salt responsive genes but also aided in the development of salt resistant transgenic plants. It has been used successfully in cotton by transferring salt responsive genes from different resources (Table 5).

Glycine betaine (GB) is an important osmoprotectant that accumulates quickly in various plants during salinity stress. Choline monoxygenase is a major catalyst used in glycine betaine synthesis. To enhance the resistant level against salt stress, a choline monoxygenase (CMO) gene (*AhCMO*) was cloned to cotton through *Agrobacterium*. The seedlings of transgenic cotton lines carried 131% more GB as compared to non-transgenic plants under normal and salinity stress respectively and this increase linked with the overexpression of *AhCMO*. Improved photosynthetic capability Fv/Fm value and lesser leaf injury was observed in transgenic plants upon salt stress exposure. (Zhang et al. 2009).

In transgenic cotton, co-expression of *AtNHX1-TsVP* genes resulted in higher seed cotton yield under saline condition that may be attributed to  $\text{Na}^+$ ,  $\text{K}^+$  and  $\text{Ca}^+$  ions accumulation in the leaves of salt effected plants. The assimilation of these cations improves ions homeostasis along with osmotic potential enabling cell to maintain higher water potential and carbon assimilation (Cheng et al. 2018). In transgenic *Arabidopsis*,  $\text{Na}^+/\text{H}^+$  antiporter gene (*GhSOS1*) was cloned from salt tolerant cotton genotype and its expression was upregulated upon exposure of NaCl salt stress. Overexpression of *GhSOS1* in

*Arabidopsis* increased salt tolerance which was proved by lower MDA level and reduced  $\text{Na}^+/\text{K}^+$  ratio in transgenic than wild type. It was suggested that *GhSOS1* gene could be utilized to develop salt tolerant transgenic plants (Chen et al. 2017).

### Seed priming and management of the nutrients

Under salt stress, sub-optimal crop establishment due to poor germination is a challenge for profitable agricultural production. Salinity stress delays and reduces the germination percentage in cotton because of osmotic stress and negative effect of  $\text{Na}^+$  and  $\text{Cl}^-$  (Sattar et al. 2010). Bradford (1986) offered seed priming technique to overcome the germination issue under salinity stress. Along with early resistance, it prepares the plants for future environmental stresses. Seed priming techniques and their effects on cotton growth has been described in Table 6.

Hydroprimed and potassium primed seeds improved germination percentage, emergence, plumule and radicle length, dried seedling and plant weight, leaf area per plant, average plant length and also reduced the time required for germination and emergence (Ahmadvand et al. 2012). Recent studies revealed that hydrogen peroxide facilitates the regulation of ABA catabolism, antagonizes the signaling of ABA, and enhances the synthesis of gibberellic acid and germination. Studies revealed that exogenous  $\text{H}_2\text{O}_2$  application improves the germination of seed via down regulation of *NCED5* and *NCED9* genes which is responsible of ABA biosynthesis. Simultaneously, it enhanced GA content via down regulation of *GA2ox1* (GA catabolism gene). The results suggested that the utilization of  $\text{H}_2\text{O}_2$  could improve the germination percentage (Kong et al. 2017).

Ionic imbalance due to reduced uptake and transport of required nutrients including potassium, calcium, nitrogen, phosphorous, magnesium, copper and iron is well documented in cotton leading to stunted plant growth and significant yield reduction (Dong 2012; Higbie et al. 2010). Potassium ion is involved in stimulation of more than 60 enzymes. It increases dry matter weight and nutrients uptake in cotton. Application of 1.5%  $\text{KNO}_3$  increased root length, shoot length, dry biomass and showed variable deposition of  $\text{K}^+$ ,  $\text{Ca}^+$  and  $\text{Na}^+$  ions in treated plants under saline condition (Shaheen et al. 2016).

The mitigation effect of humic acid (HA) was evaluated for enhancing defense response with ECe value of 3.46 and  $12.86 \text{ dS m}^{-1}$ . Humic acid application at 15 kg/ha showed pronounced effect. These findings explore the potential utilization of HA in saline soil (Rady et al. 2016). Foliar application of KCl and  $\text{NH}_4\text{NO}_3$  mixture both at vegetative and reproductive stages alleviated the adverse effects of salinity (Jabeen and Ahmad 2009). Under salt stress, cotton

**Table 5** Transgenic cotton for salt tolerance

Gene	Source	Product	Expression	Transgenic cotton performance in saline condition	References
<i>AhCMO</i>	<i>Atriplex hortensis</i>	Choline monoxygenase	Over expression	Increased salinity tolerance via producing more glycine betaine, reduced osmotic potential, malondialdehyde (MDA) deposition and electrolyte leakage	Zhang et al. (2009)
<i>AVPI</i>	<i>Arabidopsis thaliana</i>	Vacuolar pyrophosphatase		Increased ions and sugars sequestering into vacuole, stimulates the transport of auxin in the roots, develops larger root system and vigorous plant growth was observed under drought and salt stress	Pasapula et al. (2011)
<i>AtNHX1</i>	<i>Arabidopsis thaliana</i>	Vacuolar Na <sup>+</sup> /H <sup>+</sup> antiporter		Increased rate of emergence and dry matter deposition and higher seed cotton yield	Cheng et al. (2018)
<i>TsVP</i>	<i>Thellungiella halophila</i>	H <sup>+</sup> -PPase			
<i>SNAC1</i>	<i>Oryza sativa</i>	Transcriptional factors		Increased number of bolls, proline contents, improved root development and reduced rate of transpiration under salt and water stress condition	Liu et al. (2014)
<i>BetA</i>	<i>E. coli</i>	Synthesis of glycinebetaine		Increased production of glycinebetaine	Lv et al. (2004)
<i>AtHDG11</i>	<i>Arabidopsis thaliana</i>	Homeodomain-START transcription factor		Transgenic cotton exhibited well developed root system while in the leaves soluble sugar, proline contents and activities of ROS scavenging enzymes were enhanced under drought and saline condition	Yu et al. (2016)

**Table 6** Different seed priming techniques and their effects on cotton growth under saline condition

Priming agent	Improvement	References
Water	Germination, emergence, length of plumule and radicle, dry weight of seedling and plant, plant length and leaf area/plant	Ahmadvand et al. (2012)
Potassium nitrate	Germination, emergence, length of plumule and radicle, dry weight of seedling and plant, plant length and leaf area/plant	
Kinetin	Improved germination	Bozcuk (1981)
H <sub>2</sub> O <sub>2</sub>	Improved the germination through down regulation of the abscisic acid biosynthesis genes (NCED5 and NCED9)	Kong et al. (2017)
Calcium	Compensate the shoot length reduction	Kent and Läubli (1985)

growth is affected due to N deficiency caused by antagonistic effects of chloride ions on nitrate ions. Soil and foliar application of nitrogen increased salinity tolerance in cotton. It improved nitrogen uptake and its accumulation in different plant tissues and sustained higher concentration of K<sup>+</sup> and K<sup>+</sup>/Na<sup>+</sup> ratio (Luo et al. 2015). Finally, seed priming is an effective technique in cotton to improve the germination under salt stress.

## Conclusion

Globally, salinity is the serious problem for ensuring food security as more than half of countries are facing this problem. Salt stress imposes specific ions toxicity,

somatically induced water stress and nutrients imbalance which impart adverse effects on plant growth, development and ultimately crop establishment. Salt stress affects the metabolic activities of enzymes, impairs nutrients uptake and results into nutritional disorders which leads to yield reduction and fiber quality deterioration. Development of salt tolerant cotton cultivars offer the cost effective management strategy against salt stress in cotton. Maintenance of higher Ca<sup>+</sup>/Na<sup>+</sup> and K<sup>+</sup>/Na<sup>+</sup> ratios could be used as authentic selection criteria for selection of salt tolerant cotton genotypes. The prevailing genetic diversity could be used effectively for development of salt tolerant genotypes. However, genetic basis of salt tolerance is controlled by QTLs, therefore, marker assisted selection is a promising approach for indirect selection of salt tolerant genotypes.

With the advancement of molecular biology, transgenic approaches have been successfully employed for development of salt tolerance in cotton. This technique is quicker than conventional breeding. Salt tolerance could also be improved by seed priming as it overcomes the germination related issues and prepare the plants for salt tolerance and other future environmental stresses.

## References

- Abd Ella M, Shalaby EE (1993) Cotton response to salinity and different potassium-sodium ratio in irrigation water. *J Agron Crop Sci* 170:25–31
- Ahmad R, Abdullah Z (1982) Biomass production of food and fiber crops using highly saline water under desert conditions [irrigated cultivation of sugarbeets and cotton in Pakistan]. *Env Sci Res* 23:149–163
- Ahmad S, Khan N, Iqbal MZ, Hussain A, Hassan M (2002) Salt tolerance of cotton (*Gossypium hirsutum* L.). *Asian J Plant Sci* 1:715–719
- Ahmadvand G, Soleymani F, Saadatian B, Pouya M (2012) Effects of seed priming on seed germination and seedling emergence of cotton under salinity stress. *World Appl Sci J* 20:1453–1458
- Alam S, Ansari A, Khan M (2000) Nuclear Institute of Agriculture, Tando Jam. Available at <http://www.pakistaneconomist.com/issue2000/issue19&20/i&e3.htm>
- Anagholi A, Esmaeili S, Soltani V, Khaffarian H (2005) Effects of salt stress on the growth and yield of cotton at different stages of developmen. <http://agris.fao.org/agris-search/search.do?recordID=IR2012039023>
- Ansari R, Khan MA, Gul B (2007) Gainful utilization of salt affected lands: prospects and precautions. *Crop Forage Prod Saline Waters* 10:103–108
- Anschütz U, Becker D, Shabala S (2014) Going beyond nutrition: regulation of potassium homeostasis as a common denominator of plant adaptive responses to environment. *J Plant Physiol* 171:670–687
- Arora S (2017) Diagnostic properties and constraints of salt-affected soils. In: Arora S, Singh AK, Singh YP (eds) *Bioremediation of salt affected soils: an Indian perspective*. Springer, pp 41–52
- Ashraf M (2009) Biotechnological approach of improving plant salt tolerance using antioxidants as markers. *Biotechnol Adv* 27:84–93
- Ashraf M, Ahmad S (2000) Influence of sodium chloride on ion accumulation, yield components and fibre characteristics in salt-tolerant and salt-sensitive lines of cotton (*Gossypium hirsutum* L.). *Field Crops Res* 66:115–127
- Ashraf M, Kanwal S, Tahir M, Sarwar A, Ali L (2007) Differential salt tolerance of sugarcane genotypes. *Pak J Agric Sci* 44:85–89
- Aslam M, Basra S, Maqbool MA, Bilal H, UZaman Q, Bano S (2013) Physio-chemical distinctiveness and metroglyph analysis of cotton genotypes at early growth stage under saline hydroponics. *Int J Agric Biol* 15:11–1133
- Bernstein L, Hayward H (1958) Physiology of salt tolerance. *Annu Rev Plant Biol* 9:25–46
- Bozcuk S (1981) Effects of kinetin and salinity on germination of tomato, barley and cotton seeds. *Ann Bot* 48:81–84
- Bradford KJ (1986) Manipulation of seed water relations via osmotic priming to improve germination under stress conditions. *HortScience (USA)* 21:1105–1112
- Cai C, Wu S, Niu E, Cheng C, Guo W (2017) Identification of genes related to salt stress tolerance using intron-length polymorphic markers, association mapping and virus-induced gene silencing in cotton. *Sci Rep* 7:528
- Chen X, Wang J, Zhu M, Jia H, Liu D, Hao L, Guo X (2015) A cotton Raf-like *MAP3K* gene, *GhMAP3K40*, mediates reduced tolerance to biotic and abiotic stress in *Nicotiana benthamiana* by negatively regulating growth and development. *Plant Sci* 240:10–24
- Chen X et al (2017) *GhSOS1*, a plasma membrane  $\text{Na}^+/\text{H}^+$  antiporter gene from upland cotton, enhances salt tolerance in transgenic *Arabidopsis thaliana*. *PLoS ONE* 12:e0181450
- Cheng C, Zhang Y, Chen X, Song J, Guo Z, Li K, Zhang K (2018) Co-expression of *AtNHX1* and *TsVP* improves the salt tolerance of transgenic cotton and increases seed cotton yield in a saline field. *Mol Breed* 38:19
- Chu X et al (2015) The cotton WRKY gene *GhWRKY41* positively regulates salt and drought stress tolerance in transgenic *Nicotiana benthamiana*. *PLoS ONE* 10:e0143022
- Conde A, Chaves MM, Gerós H (2011) Membrane transport, sensing and signaling in plant adaptation to environmental stress. *Plant Cell Physiol* 52:1583–1602
- Czégény G, Wu M, Dér A, Eriksson LA, Strid Å, Hideg É (2014) Hydrogen peroxide contributes to the ultraviolet-B (280–315 nm) induced oxidative stress of plant leaves through multiple pathways. *FEBS Lett* 588:2255–2261
- Dai J, Duan L, Dong H (2014) Improved nutrient uptake enhances cotton growth and salinity tolerance in saline media. *J Plant Nutr* 37:1269–1286
- Dhandapani G et al (2015) A gene encoding cold-circadian rhythm-RNA binding-like protein (CCR-Like) from upland Cotton (*Gossypium hirsutum* L.) confers tolerance to abiotic stresses in transgenic tobacco. *Plant Mol Biol Rep* 33:22–42
- Ding M et al (2010) Salt-induced expression of genes related to  $\text{Na}^+/\text{K}^+$  and ROS homeostasis in leaves of salt-resistant and salt-sensitive poplar species. *Plant Mol Biol* 73:251–269
- Dong H (2012) Combating salinity stress effects on cotton with agronomic practices. *Afr J Agric Res* 7:4708–4715
- Du L, Cai C, Wu S, Zhang F, Hou S, Guo W (2016) Evaluation and exploration of favorable QTL alleles for salt stress related traits in cotton cultivars (*G. hirsutum* L.). *PLoS ONE* 11:e0151076
- El Saidi M, Hegazy W (1980) Effect of using saline water for irrigation at different growth stages on yield and some physiological processes of cotton plant. *Agric Res Rev* 58:337–355
- Fan X et al (2015) Transcriptome-wide identification of salt-responsive members of the WRKY gene family in *Gossypium aridum*. *PLoS ONE* 10:e0126148
- Fernandes F, Arrabaça M, Carvalho L (2004) Sucrose metabolism in *Lupinus albus* L. under salt stress. *Biol Plantarum* 48:317
- Foyer CH, Noctor G (2000) Tansley review no. 112 oxygen processing in photosynthesis: regulation and signalling. *New Phytol* 146:359–388
- Gao S-Q et al (2009) A cotton (*Gossypium hirsutum*) DRE-binding transcription factor gene, GhDREB, confers enhanced tolerance to drought, high salt, and freezing stresses in transgenic wheat. *Plant cell Rep* 28:301–311
- Golan-Goldhirsh A, Hankamer B, Lips S (1990) Hydroxyproline and proline content of cell walls of sunflower, peanut and cotton grown under salt stress. *Plant Sci* 69:27–32
- Gong W, Xu F, Sun J, Peng Z, He S, Pan Z, Du X (2017) iTRAQ-based comparative proteomic analysis of seedling leaves of two upland cotton genotypes differing in salt tolerance. *Front Plant Sci* 8:2113
- Guo YH, Yu YP, Wang D, Wu CA, Yang GD, Huang JG, Zheng CC (2009) GhZFP1, a novel CCCH-type zinc finger protein from cotton, enhances salt stress tolerance and fungal disease

- resistance in transgenic tobacco by interacting with GZIRD21A and GZIPR5. *New Phytol* 183:62–75
- Guo-Wei Z, Hai-Ling L, Lei Z, Bing-Lin C, Zhi-Guo Z (2011) Salt tolerance evaluation of cotton (*Gossypium hirsutum*) at its germinating and seedling stages and selection of related indices. *Yingyong Shengtai Xuebao* 22:2045–2053
- Higbie SM, Wang F, Stewart JM, Sterling TM, Lindemann WC, Hughs E, Zhang J (2010) Physiological response to salt (NaCl) stress in selected cultivated tetraploid cottons. *Int J Agron* 2010:1–12
- Higinbotham N (1973) Electropotentials of plant cells. *Annu Rev Plant Physiol* 24:25–46
- Hossain M (2010) Global warming induced sea level rise on soil, land and crop production loss in Bangladesh. In: 19th world congress of soil science, soil solutions for a changing world, Brisbane. <http://www.ars.usda.gov/Services/docs.htm>
- Jabeen R, Ahmad R (2009) Alleviation of the adverse effects of salt stress by foliar application of sodium antagonistic essential minerals on cotton (*Gossypium hirsutum*). *Pak J Bot* 41:2199–2208
- Jafri AZ, Ahmad R (1995) Effect of soil salinity on leaf development, stomatal size and its distribution in cotton. *Pak J Bot* 27:297–303
- Jamil A, Riaz S, Ashraf M, Foolad M (2011) Gene expression profiling of plants under salt stress. *Crit Rev Plant Sci* 30:435–458
- Jin LG, Li H, Liu JY (2010) Molecular characterization of three ethylene responsive element binding factor genes from cotton. *J Integr Plant Biol* 52:485–495
- Johnson KL, Jones BJ, Bacic A, Schultz CJ (2003) The fasciclin-like arabinogalactan proteins of Arabidopsis. A multigene family of putative cell adhesion molecules. *Plant Physiol* 133:1911–1925
- Joseph EA, Mohanan K (2013) A study on the effect of salinity stress on the growth and yield of some native rice cultivars of Kerala state of India. *Agric For Fish* 2:141–150
- Kafi M, Moayedi A, Jafari M (2018) The sensitivity of grain Sorghum (*Sorghum bicolor* L.) developmental stages to salinity stress: an integrated approach. *J Agric Sci Technol* 15:723–736
- Katerji N, Van Hoorn J, Hamdy A, Mastrorilli M (2000) Salt tolerance classification of crops according to soil salinity and to water stress day index. *Agric Water Manag* 43:99–109
- Keisham M, Mukherjee S, Bhatla S (2018) Mechanisms of sodium transport in plants—progresses and challenges. *Int J Mol Sci* 19:647
- Kent L, Läuchli A (1985) Germination and seedling growth of cotton: salinity-calcium interactions. *Plant. Cell Environ* 8:155–159
- Khan A, Qureshi R, Ahmad N (1995) Performance of cotton cultivars in saline growth media at germination stage. *Sarhad J Agric* 11:643–646
- Khan A, Qureshi R, Ahmad N (1998a) Performance of cotton cultivars as affected by types of salinity I, Growth and yield. *Sarhad J Agric* 14:73–77
- Khan MA, Ungar IA, Showalter AM, Dewald HD (1998b) NaCl-induced accumulation of glycinebetaine in four subtropical halophytes from Pakistan. *Physiol Plant* 102:487–492
- Khorsandi F, Anaghli A (2009) Reproductive compensation of cotton after salt stress relief at different growth stages. *J Agron Crop Sci* 195:278–283
- Kong X, Luo Z, Zhang Y, Li W, Dong H (2017) Soaking in H<sub>2</sub>O<sub>2</sub> regulates ABA biosynthesis and GA catabolism in germinating cotton seeds under salt stress. *Acta Physiol Plant* 39:2
- Lee EK, Kwon M, Ko J-H, Yi H, Hwang MG, Chang S, Cho MH (2004) Binding of sulfonylurea by *AtMRP5*, an Arabidopsis multidrug resistance-related protein that functions in salt tolerance. *Plant Physiol* 134:528–538
- Lee MH et al (2013) Divergences in morphological changes and antioxidant responses in salt-tolerant and salt-sensitive rice seedlings after salt stress. *Plant Physiol Biochem* 70:325–335
- Leidi EO (1994) Genotypic variation of cotton in response to stress by NaCl or PEG. In: Peeters MC (ed) Cotton biotechnology, REUR technical series, vol 32. FAO, Rome, pp 67–73
- Leidi E, Saiz J (1997) Is salinity tolerance related to Na accumulation in upland cotton (*Gossypium hirsutum*) seedlings? *Plant Soil* 190:67–75
- Li G, Tai F-J, Zheng Y, Luo J, Gong S-Y, Zhang Z-T, Li X-B (2010) Two cotton Cys2/His2-type zinc-finger proteins, *GhDi19-1* and *GhDi19-2*, are involved in plant response to salt/drought stress and abscisic acid signaling. *Plant Mol Biol* 74:437–452
- Li Q, Xiao G, Zhu Y-X (2014) Single-nucleotide resolution mapping of the *Gossypium raimondii* transcriptome reveals a new mechanism for alternative splicing of introns. *Mol Plant* 7:829–840
- Li W et al (2015) Identification of early salt stress responsive proteins in seedling roots of upland cotton (*Gossypium hirsutum* L.) employing iTRAQ-based proteomic technique. *Front Plant Sci* 6:732
- Liang C et al (2016) GhABF2, a bZIP transcription factor, confers drought and salinity tolerance in cotton (*Gossypium hirsutum* L.). *Sci Rep* 6:35040
- Liu G, Li X, Jin S, Liu X, Zhu L, Nie Y, Zhang X (2014) Overexpression of rice NAC gene SNAC1 improves drought and salt tolerance by enhancing root development and reducing transpiration rate in transgenic cotton. *PLoS ONE* 9:e86895
- Liu X, Song Y, Xing F, Wang N, Wen F, Zhu C (2016) *GhWRKY25*, a group I WRKY gene from cotton, confers differential tolerance to abiotic and biotic stresses in transgenic *Nicotiana benthamiana*. *Protoplasma* 253:1265–1281
- Longenecker D (1974) The influence of high sodium in soils upon fruiting and shedding, boll characteristics, fiber properties, and yields of two cotton species. *Soil Sci* 118:387–396
- Lu W, Chu X, Li Y, Wang C, Guo X (2013) Cotton *GhMKK1* induces the tolerance of salt and drought stress, and mediates defence responses to pathogen infection in transgenic *Nicotiana benthamiana*. *PLoS ONE* 8:e68503
- Luo X et al (2013) Synergistic effects of *GhSOD1* and *GhCAT1* overexpression in cotton chloroplasts on enhancing tolerance to methyl viologen and salt stresses. *PLoS ONE* 8:e54002
- Luo Z, Kong X, Dai J, Dong H (2015) Soil plus foliar nitrogen application increases cotton growth and salinity tolerance. *J Plant Nutr* 38:443–455
- Lv S, Yin X, Zhang K, Zhang J (2004) Agrobacterium-mediated transformation of shoot apex of cotton and production of transgenic plants carrying betA gene. *Gaojishu Tongxun* 14:20–25
- Ma X, Dong H, Li W (2011) Genetic improvement of cotton tolerance to salinity stress. *Afr J Agric Res* 6:6797–6803
- Ma L, Hu L, Fan J, Amombo E, Khaldun A, Zheng Y, Chen L (2017) Cotton GhERF38 gene is involved in plant response to salt/drought and ABA. *Ecotoxicology* 26:841–854
- Maas EV, Hoffman GJ (1977) Crop salt tolerance—current assessment. *J Irrig Drain Div* 103:115–134
- Manchandia AM, Banks SW, Gossett DR, Bellaire BA, Lucas MC, Millhollon EP (1999) The influence of  $\alpha$ -amanitin on the NaCl-induced up-regulation of antioxidant enzyme activity in cotton callus tissue. *Free Radic Res* 30:429–438
- Mansour M, Salama K, Ali F, Abou Hadid A (2005) Cell and plant responses to NaCl in *Zea mays* L. cultivars differing in salt tolerance. *Gen Appl Plant Physiol* 31:29–41
- Meloni DA, Oliva MA, Ruiz HA, Martinez CA (2001) Contribution of proline and inorganic solutes to osmotic adjustment in cotton under salt stress. *J Plant Nutr* 24:599–612

- Meng C, Cai C, Zhang T, Guo W (2009) Characterization of six novel NAC genes and their responses to abiotic stresses in *Gossypium hirsutum* L. *Plant Sci* 176:352–359
- Meng H-B, Jiang S-S, Hua S-J, Lin X-Y, Li Y-L, Guo W-L, Jiang L-X (2011) Comparison between a tetraploid turnip and its diploid progenitor (*Brassica rapa* L.): the adaptation to salinity stress. *Agric Sci China* 10:363–375
- Mojid M, Mia M, Saha A, Tabriz S (2013) Growth stage sensitivity of wheat to irrigation water salinity. *J Bangladesh Agric Univ* 11:147–152
- Naidoo G, Naidoo Y (2001) Effects of salinity and nitrogen on growth, ion relations and proline accumulation in *Triglochin bulbosa*. *Wetl Ecol Manag* 9:491–497
- Noreen Z, Ashraf M (2009) Assessment of variation in antioxidative defense system in salt-treated pea (*Pisum sativum*) cultivars and its putative use as salinity tolerance markers. *J Plant Physiol* 166:1764–1774
- Oluoch G et al (2016) QTL mapping for salt tolerance at seedling stage in the interspecific cross of *Gossypium tomentosum* with *Gossypium hirsutum*. *Euphytica* 209:223–235
- Pasapula V et al (2011) Expression of an Arabidopsis vacuolar H<sup>+</sup>-pyrophosphatase gene (AVP1) in cotton improves drought- and salt tolerance and increases fibre yield in the field conditions. *Plant Biotechnol J* 9:88–99
- Peng J et al (2016a) Effects of soil salinity on sucrose metabolism in cotton leaves. *PLoS ONE* 11:e0156241
- Peng J et al (2016b) Effects of Soil Salinity on Sucrose Metabolism in Cotton Fiber. *PLoS ONE* 11:e0156398
- Pervaiz S, Saqib M, Akhtar J, Riaz MA, Anwar-ul-Haq M, Nasim M (2007) Comparative growth and leaf ionic composition of four cotton (*Gossypium hirsutum* L.) genotypes in response to salinity. *Pak J Agric Sci* 44:15–20
- Quan RD, Shang M, Zhang H, Zhao Y ZJ (2004) Engineering of enhanced glycine betaine synthesis improves drought tolerance in maize. *Plant Biotechnol J* 2:477–486
- Rady M, El-Mageed TA, Abdurrahman H, Mahdi A (2016) Humic acid application improves field performance of cotton (*Gossypium barbadense* L.) under saline conditions. *J Animal Plant Sci* 26:485–493
- Rafique A, Salim M, Hussain M, Gelani S (2003) Morpho-physiological response of cotton (*Gossypium hirsutum* L.) cultivars to variable edaphic conditions. *Pak J Life Soc Sci* 1:5–8
- Rajguru SN, Banks SW, Gossett DR, Lucas MC, Fowler TE, Millhollon EP (1999) Antioxidant response to salt stress during fiber development in cotton ovules. *J Cotton Sci* 3(1):11–18
- Rathert G (1983) Effects of high salinity stress on mineral and carbohydrate metabolism of two cotton varieties. *Plant Soil* 73:247–256
- Rathert G, Doering H (1983) Influence of extreme K: Na ratios and high substrate salinity on plant metabolism of crops differing in salt tolerance: VIII. Ion-specific salinity effects on carbohydrates and degradative enzymes of two soybean varieties. *J Plant Nutr* 6:583–595
- Richards LA (1954) Diagnosis and improvement of saline alkali soils, vol 60. US Department of Agriculture Handbook, Washington
- Rontein D, Basset G, Hanson AD (2002) Metabolic engineering of osmoprotectant accumulation in plants. *Metab Eng* 4:49–56
- Saddiqe Z, Javeria S, Khalid H, Farooq A (2016) Effect of salt stress on growth and antioxidant enzymes in two cultivars of maize (*Zea mays* l.). *Pak J Bot* 48:1361–1370
- Saeed M, Wangzhen G, Tianzhen Z (2014) Association mapping for salinity tolerance in cotton (*Gossypium hirsutum* L.) germplasm from US and diverse regions of China. *Aust J Crop Sci* 8:338
- Saqib M, Akhtar J, Pervaiz S, Qureshi R, Aslam M (2002) Comparative growth performance of five cotton (*Gossypium hirsutum* L.) genotypes against different levels of salinity. *Pak J Agri Sci* 39:69–75
- Sattar S, Hussain T, Javaid A (2010) Effect of NaCl salinity on cotton (*Gossypium arboreum* L.) grown on MS medium and in hydroponic cultures. *J Animal Plant Sci* 20:87–89
- Seemann JR, Sharkey TD (1986) Salinity and nitrogen effects on photosynthesis, ribulose-1, 5-bisphosphate carboxylase and metabolite pool sizes in *Phaseolus vulgaris* L. *Plant Physiol* 82:555–560
- Shabala SN, Lew RR (2002) Turgor regulation in osmotically stressed Arabidopsis epidermal root cells. Direct support for the role of inorganic ion uptake as revealed by concurrent flux and cell turgor measurements. *Plant Physiol* 129:290–299
- Shah ST, Pang C, Fan S, Song M, Arain S, Yu S (2013) Isolation and expression profiling of GhNAC transcription factor genes in cotton (*Gossypium hirsutum* L.) during leaf senescence and in response to stresses. *Gene* 531:220–234
- Shah S, Houborg R, McCabe M (2017) Response of chlorophyll, carotenoid and SPAD-502 measurement to salinity and nutrient stress in wheat (*Triticum aestivum* L.). *Agronomy* 7:61
- Shaheen HL, Shahbaz M, Ullah I, Iqbal MZ (2012) Morpho-physiological responses of cotton (*Gossypium hirsutum* L.) to salt stress. *Int J Agric Biol* 14:980–984
- Shaheen HL, Iqbal M, Azeem M, Shahbaz M, Shehzadi M (2016) K-priming positively modulates growth and nutrient status of salt-stressed cotton (*Gossypium hirsutum*) seedlings. *Arch Agron Soil Sci* 62:759–768
- Sharif A, Rasul E, Nisar A, Sadiq M (1999) Response of Maize (*Zea mays* L.) genotypes to NaCl salinity induced at various growth stages of crop. *Pak J Bio Sci* 2:606–608
- Shi W, Hao L, Li J, Liu D, Guo X, Li H (2014a) The *Gossypium hirsutum* WRKY gene *GhWRKY39-1* promotes pathogen infection defense responses and mediates salt stress tolerance in transgenic *Nicotiana benthamiana*. *Plant Cell Rep* 33:483–498
- Shi W, Liu D, Hao L, C-a W, Guo X, Li H (2014b) *GhWRKY39*, a member of the WRKY transcription factor family in cotton, has a positive role in disease resistance and salt stress tolerance. *PTOC* 118:17–32
- Silberbush M, Ben-Asher J (1987) The effect of salinity on parameters of potassium and nitrate uptake of cotton. *Commun Soil Sci Plant Anal* 18:65–81
- Simoes WL, Calgaro M, Coelho DS, Santos D, Souza M (2016) Growth of sugar cane varieties under salinity. *Rev Ceres* 63:265–271
- Soliman M, Farah M, Anter I (1980) Seed germination and root growth of corn and cotton seedlings as affected by soil texture and salinity of irrigation water. *Agrochimica* 24:113–120
- Sta-Baba R, Hachicha M, Mansour M, Nahdi H, Kheder MB (2010) Response of onion to salinity. *Afr J Plant Sci Biotechnol* 4:7–12
- Sun Z et al (2018) Identification of SNPs and candidate genes associated with salt tolerance at the seedling stage in cotton (*Gossypium hirsutum* L.). *Front Plant Sci* 9:1–12
- Theodoulou FL (2000) Plant ABC transporters. *Biochimica et Biophysica Acta (BBA)-Biomembranes* 1465:79–103
- Thomas J (1980) Osmotic and specific salt effects on growth of cotton 1. *Agron J* 72:407–412
- Wang J, Wang D, Fan W, Song G, Wang S, Ye W (2011) The characters of salt-tolerance at different growth stages in cotton. *Shengtai Xuebao Acta Ecol Sin* 31:3720–3727
- Wang Z et al (2012) QTL analysis of Na<sup>+</sup> and K<sup>+</sup> concentrations in roots and shoots under different levels of NaCl stress in rice (*Oryza sativa* L.). *PLoS ONE* 7:51202
- Wang W et al (2016) Characterization, expression, and functional analysis of a novel NAC gene associated with resistance to Verticillium Wilt and abiotic stress in cotton. *G3 (Bethesda)* 6:3951–3961



- Wang N et al (2017) Relative contribution of  $\text{Na}^+/\text{K}^+$  homeostasis, photochemical efficiency and antioxidant defense system to differential salt tolerance in cotton (*Gossypium hirsutum* L.) cultivars. *Plant Physiol Biochem* 119:121–131
- Wu C-A, Yang G-D, Meng Q-W, Zheng C-C (2004) The cotton GhNHX1 gene encoding a novel putative tonoplast  $\text{Na}^+/\text{H}^+$  antiporter plays an important role in salt stress. *Plant Cell Physiol* 45:600–607
- Xue T, Li X, Zhu W, Wu C, Yang G, Zheng C (2008) Cotton metallothionein *GhMT3a*, a reactive oxygen species scavenger, increased tolerance against abiotic stress in transgenic tobacco and yeast. *J Exp Bot* 60:339–349
- Yfoulis A, Fasoulas A (1973) Interactions of genotype and temperature on cotton boll period and their implication in breeding. *Exp Agric* 9:193–201
- Yu LH et al (2016) Arabidopsis EDT1/HDG11 improves drought and salt tolerance in cotton and poplar and increases cotton yield in the field. *Plant Biotechnol J* 14:72–84
- Zhang H, Dong H, Li W, Sun Y, Chen S, Kong X (2009) Increased glycine betaine synthesis and salinity tolerance in AhCMO transgenic cotton lines. *Mol Breed* 23:289–298
- Zhang L et al (2011) A cotton group C MAP kinase gene, GhMPK2, positively regulates salt and drought tolerance in tobacco. *Plant Mol Biol* 77:17–31
- Zhang L, Zhang G, Wang Y, Zhou Z, Meng Y, Chen B (2013) Effect of soil salinity on physiological characteristics of functional leaves of cotton plants. *J Plant Res* 126:293–304
- Zhang L, Ma H, Chen T, Pen J, Yu S, Zhao X (2014) Morphological and physiological responses of cotton (*Gossypium hirsutum* L.) plants to salinity. *PLoS ONE* 9:e112807
- Zhang F, Li S, Yang S, Wang L, Guo W (2015) Overexpression of a cotton annexin gene, GhAnn1, enhances drought and salt stress tolerance in transgenic cotton. *Plant Mol Biol* 87:47–67
- Zhang F et al (2016) Genetic regulation of salt stress tolerance revealed by RNA-Seq in cotton diploid wild species *Gossypium davidsonii*. *Sci Rep* 6:20582
- Zhang B, Chen X, Shu X, Lu N, Wang X, Yang X, Ye W (2018) Transcriptome analysis of *Gossypium hirsutum* L. reveals different mechanisms among NaCl, NaOH and  $\text{Na}_2\text{CO}_3$  stress tolerance. *Sci Rep* 8:13527
- Zhao Q, Zhang H, Wang T, Chen S, Dai S (2013) Proteomics-based investigation of salt-responsive mechanisms in plant roots. *J Proteom* 82:230–253
- Zhao Y et al (2016) SSR-based association mapping of salt tolerance in cotton (*Gossypium hirsutum* L.). *GMR* 15:15027370
- Zhou L, Wang N-N, Kong L, Gong S-Y, Li Y, Li X-B (2014) Molecular characterization of 26 cotton WRKY genes that are expressed differentially in tissues and are induced in seedlings under high salinity and osmotic stress. *PCTOC* 119:141–156

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.