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Review article

Technology and field management for controlling soil salinity effects on cotton

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Abstract

Soil salinity is a major threat to cotton production worldwide. Excessive salt in the soil leads to a series of physiological and biochemical metabolic disorders in cotton plants mainly as a result of osmotic effects (dehydration), nutritional imbalance and toxicity of salt ions (Na^+ and CI). The metabolic disorders may finally reduce plant growth and lint yield and quality, particularly in conditions of high salinity. Basically, combating the effects of salinity stress on cotton plants involves two main strategies: one is to improve salt tolerance through genetic breeding and chemical or biological treatment, the other is to avoid or alleviate salinity stress on cotton, with a focus on recent advances in agronomic techniques for managing salinity in the root zone. We recommend a comprehensive use of agronomic practices such as suitable cultivars, proper irrigation and fertilization, seed pretreatment, furrow seeding, plastic mulching and induction of unequal salt distribution in the root-zone to combat salinity stress. Further research should focus on exploration and understanding of the uptake and efficient use of water and nutrients in saline soils. Research should also focus on the development of new products for cotton growing in saline soils like new foliar and specific slow-release fertilizers and commercial plant growth regulators to improve salt tolerance.

Keywords: Cotton, Salinity stress, Salt tolerance, Agronomic practice, Unequal Salt distribution.

Abbreviations: ECe_electrical conductivity of a saturated-paste extract; PHCA _polyhydroxycarboxylic acid; COR_Coronatine; CAT_catalase; POD_peroxidase; GR_glutathione reductase; DPPH_1,1-diphenyl-2- picrylhydrazyl; IAA_indole acetic acid, ABA_abscisic acid; VAM_vesicular arbuscular mycorrhizal.

Introduction

Soil salinity has been a major concern to global agriculture throughout human history (Lobell et al., 2007). In recent times, it has become even more prevalent as the intensity of land use increases globally (Haque, 2006). Cotton is an important cash crop worldwide. Although it is classified as one of the most salt-tolerant crops and considered a pioneer crop in reclamation of saline soils (Maas, 1990), its growth and yield and fiber quality are negatively affected by excessive salts in the soil (Maas and Hoffman, 1977; Qadir and Shams, 1997; Higbie et al., 2010). Soil salinity are usually expressed by ECe (electrical conductivity of a saturated-paste extract), and ECes around 7.7, 12 and 17 dS/m are referred to as low, moderate and high salinity levels, respectively (Chen et al., 2009; Maas and Grattan, 1999). In general, soil salinity delays and reduces germination and emergence, decreases cotton shoot growth, and may finally lead to reduced seed cotton yield and fiber quality at moderate to high salinity levels (Khorsandi and Anagholi, 2009). However, the cotton plant has a complete self-protection system against salinity (Ashraf, 2002), which can be activated through a series of morphological, physiological and biochemical changes in conditions of salt stress. Over the last thirty years, a number of studies have been conducted on the response of cotton plants to saline soils and/or irrigation with saline water. Progress has been made in all

aspects of plant-soil salinity of cotton. Understanding how plants respond to salinity can play a major role in stabilizing crop performance under saline conditions and in the protection of natural vegetation. Adequate management techniques and plant genetic breeding are the tools for improving resource use efficiency (including water) in plants. Since plant response to salinity and genetic improvement of salinity tolerance have been reviewed (Ashraf, 2002; Ahmad et al., 2002; Lubbers et al., 2007; Gorham et al., 2009; Ma et al., 2012), the present review covers research work on combating salinity stress effects on cotton, with a focus on comprehensive utilization of agronomic practices.

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Effects of salinity stress on plant growth and physiology

Understanding the effects of salinity stress on cotton growth and physiology is a prerequisite to successful salinity management and control. Salinity effects on cotton plant may vary with the growth stage and extent and time of salinity stress. Biological or economic yield reduction is the main effect of salinity at the whole-plant level, and is usually attributed to various physiological and biochemical processes at the cellular or molecular levels (Meloni et al., 2003; Nawaz et al., 2010; Munns and Tester, 2008).

Effects of salinity stress on germination and seedling growth

Although salinity effects occur at almost all growth stages, including germination, seedling, vegetative and mature stages of field-grown cotton, it is generally believed that germination and young seedling stages are more sensitive to salinity stress than other stages (Ahmad et al., 2002). Seed germination and emergence of cotton are generally delayed and reduced by salinity (Qadir and Shams, 1997). In sand culture, seed germination was 68-89% at 150 mM and 24-40% at 250 mM NaCl, but in soil, the germination was 72-89% at 15 dS/m and 20-53% at 25 dS/m (Khan et al., 1995). A recent study conducted in potted saline soil (Dong et al., 2009b) showed more severe inhibition of emergence and stand establishment than reported above. There were significant linear correlations between soil salinity and emergence rate expressed as DAP (days after planting) (DAP = 0.8011ECe + 2.2145, $R^2 =$ 0.9536), emergence rate (ER, %) (ER = -7.0701ECe + 115.9, $R^2 = 0.9711$), and stand establishment rate (SER, %) (SER = -7.8424ECe + 106.7, $R^2 = 0.9482$) (Dong et al., 2009b). Normal emergence and stand establishment were obtained when soil salinity was lower than 5 dS/m. Rates of emergence and stand establishment were reduced to 60-78% and 45-55%, respectively, when soil ECe was 5-7.5 dS/m. The emergence and stand establishment rates were only about 40 and <30%, respectively, in saline fields with salinity higher than 10 dS/m (Dong et al., 2009b). Salinity over 7.7 dS/m also affects cotton growth and development. The appearance of salinity stressed cotton plants are usually similar to the appearance of drought-stressed cotton plants, showing smaller and dark blue, or green, leaves. This is mainly due to increased osmotic pressure of the soil solution leading to physiological dryness and accumulation of one or more elements likely to hinder uptake of one or more nutrient elements (Praharaj and Rajendran, 2004). As soil salinity increases, leaves become brittle and necrotic, leading to stunted growth and poor yield. Reduced availability of N, P, Mn, Cu, Zn and Fe, high osmotic pressure, poor air and water movement and low microbial activity are also problems associated with saline soils (Pessarakli, 2001).

Physiological response to salinity stress

Soil salinity stress reduces plant growth mainly through three mechanisms-osmotically induced water stress, specific ion toxicity due to high concentration of sodium and chloride ions, and nutrient ion imbalance due to high level of Na⁺ and Cl⁻ which reduces the uptake of K^+ , NO⁻, PO_4^{3-} , etc (Greenway and Munns, 1980). Alteration of cell wall extensibility (Pritchard et al., 1991) and accumulation of salt in the apoplast (Flowers et al., 1991) were also reported as possible causes. In saline soils (≥4 dS/m at 25°C) (Richards, 1954), too much salt in the soil environment makes the soil solution maintain such a low osmotic potential that cotton can not take up enough water, which leads to osmotic or water-deficit effect of salinity stress (Khan et al., 2004). Cotton plants, however, can accumulate compatible solutes or osmoprotectants, which serve as nontoxic solutes for cytoplasmic osmoregulation to cope with the low osmotic potential in the soil (Zhang et al., 2009). Both cellular and metabolic processes involved in osmotic stress due to salinity are similar to those due to drought. The rate at which new leaves are produced depends largely on the water potential of the soil solution, in the same way as for a drought-stressed plant (Nawaz et al., 2010). Reductions in the rate of leaf and root growth are probably due to factors associated with water stress (Munns, 2002). The degree of growth inhibition due to

osmotic stress depends on the time and scale of the response, the particular tissue and species in question, and whether the stress treatments are imposed abruptly or slowly (Ashraf, 1994; Munns et al., 2002). There were considerable similarities and moderate differences in mechanisms of photosynthetic inhibition between the two kinds of stress (Tang et al., 2007). Transcript-profiling of plants subjected to drought and salt suggest that plants perceive and respond to these stresses by quickly altering gene expression in parallel with physiological and biochemical alterations; this occurs even under mild to moderate stress. It is apparent that both stresses lead to down-regulation of some photosynthetic genes, with most of the changes being small, possibly reflecting the mild stress imposed. When compared with drought, salt stress affected more genes and more intensely, possibly reflecting the combined effects of dehydration and osmotic stress in salt-stressed plants (Chaves et al., 2009). There are 12 main soluble salts made up of cations (Na⁺, Ca²⁺ and Mg²⁺) and anions $(CO_3^{2-}, HCO_3^{-}, Cl^{-} and SO_4^{--})$ in saline soils (Pessarakli, 2001; Haque, 2006). Toxicity occurs as a result of uptake and accumulation of certain toxic ions from the saline soil or irrigation water. These toxic constituents include mainly sodium, chloride and sulphate. Although chloride and sulphate are essential elements, their content in the saline soil is far more than required for normal growth of plants. They can reduce crop productivity and eventually cause crop failures (Nawaz et al., 2010). The salt taken up by plants concentrates in the old leaves (Munns, 2002); continued transport of salt into transpiring leaves over a long period of time eventually results in very high Na⁺ and Cl⁻ concentrations, and the leaves die (Munns, 2005). The cause of the injury is probably due to rapid accumulation of Na⁺ and Cl⁻ in the cytoplasm and inhibition of enzyme activity. Alternatively, they might build up in the cell walls and dehydrate the cell (Munns, 2005). The Cl⁻ is more toxic than Na⁺ in a number of plant species including cotton (Luo et al., 2002; Tavakkoli et al., 2010). Concentrations of Na⁺ and Cl in cotton roots, xylem sap and leaf increased with increasing concentration of NaCl in the soil environment (Hirayama, 1987); a large quantity of Na⁺ and Cl⁻ poured into the cells and destroyed the ion balance in the cytoplasm, particularly the Ca^{2+} balance. High concentrations of Na⁺ can replace bound Ca^{2+} in plasma membrane and cell membrane system, when the ratio of Na^+/Ca^{2+} increased, finally damaging the membrane structural integrity and function. As a result, a dramatic increase in free cytoplasmic Ca²⁺ impaired cellular metabolism (Hirayama, 1987). However, plants can adapt to salinity through osmotic stress tolerance, Na⁺ or Cl⁻ exclusion, and the tolerance of tissue to accumulated Na⁺ or Cl⁻ (Munns and Tester, 2008). Cotton, particularly the salinity-tolerant cultivar has also evolved many mechanisms in response to uptake and accumulation of salt ions $(Na^+ and Cl^-)$ under salinity stress. One of the most important mechanisms is to reduce excessive Na⁺ in the cytoplasm. Sodium ion extrusion from the cytosol and partitioning within the vacuole are two main ways to reduce excessive Na⁺ in the cytoplasm (Lin et al., 1997; Lv et al., 2008). The plasma membrane H^+ -ATPase generates the potential required to drive in positive ions into the cell (Lin et al., 1997). In vacuolar membranes, another H⁺-ATPase creates the potential required for the uptake of K⁺ and/or Na⁺ into the vacuole by the activity of transporters like a Na^{+}/H^{+} antiporter, which would regulate cytoplasmic Na^{+} sequestering it into the vacuole (Gorham et al., 2009). The compartmentation of Na⁺ into the vacuole, through vacuolar Na^{+}/H^{+} antiporters provides an efficient mechanism to avert the deleterious effects of Na⁺ in the cytosol and maintain an osmotic potential by using Na⁺ (and chloride) accumulated in the vacuole to drive water uptake into cells (Apse et al., 1999). More research efforts have been made to increase the vacuolar osmotic pressure with the concomitant decrease in water potential in favor of water movement from soil into plant root cells in recent years. Two approaches have been used to increase solute contents in plant vacuoles (Pasapula et al., 2011). The first approach involves increasing the activity of a vacuolar sodium proton (Na⁺/H⁺) antiporter that mediates the exchange of cytosolic Na⁺ for vacuolar H⁺. The second approach involves increasing the activity of the H⁺ pump on the vacuolar membrane to move more H⁺ into the vacuoles, therefore generating a higher proton electrochemical gradient (DIH⁺) that can be used to energize secondary transporters, including vacuolar Na⁺/H⁺ antiporters. Both approaches enhance Na⁺ accumulation in the vacuoles and reduce the potential of Na⁺ toxicity in the cytoplasm, leading to higher salt tolerance in transgenic plants. A transgenic cotton plant was developed to over-express AtNHX1, an Arabidopsis vacuolar Na^{+}/H^{+} antiporter by He et al. (2005, 2007). Over-expression of the tonoplast Na⁺/H⁺ antiporters increases sodium transfer into vacuoles, which leads to higher vacuolar salt concentration and therefore higher salt tolerance. Similarly, cotton plants over-expressing TsVP, an H⁺- PPase gene cloned from Thellungiella halophila, transports more Na⁺ into vacuoles and significantly enhanced the salt tolerance of cotton (Lv et al., 2008). The Arabidopsis AVP1 gene encodes a vacuolar pyrophosphatase that functions as a proton pump on the vacuolar membrane. Pasapula et al. (2011) reported that increased expression of the vacuolar membrane-bound H⁺ pump can indeed lead to increased salt tolerance in transgenic cotton, and that AVP1-expressing cotton produces more fiber under field conditions (Pasapula et al., 2011). It is believed that the sequestering of Na⁺ in the vacuoles confers two advantages: reduced toxic levels of Na⁺ in cytosol, and increased osmotic potential of the vacuole and therefore a more negative water potential that aids water uptake by the cells and water retention under high salt conditions (Lubbers et al., 2007). Osmotic stress may result in the disturbance of the plant water relations in the uptake and utilization of essential nutrients, and also in toxic ion accumulation (Gouia et al., 1994). As a result of these changes, the activities of various enzymes and plant metabolism are affected (Munns, 2002). The competition and interactions of soluble salts with mineral nutrients may cause considerable nutrient imbalances and deficiencies (Rathert, 1982). Ionic imbalance occurs in the cells due to over accumulation of Na⁺ and Cl⁻ and reduced uptake of other mineral nutrients, such as K⁺, Ca²⁺, and Mn²⁺ (Karimi et al., 2005). High sodium to potassium ratio due to accumulation of high amounts of sodium ions inactivates enzymes and affects metabolic processes in plants (Booth and Beardall, 1991). It is generally accepted that Ca2+ plays an important role in alleviating salinity damage by protecting the cell membrane structure of cotton. Cramer (1987) reported that NaCl stress severely inhibited root absorption, transportation and distribution of Ca²⁺ and K⁺ in cotton. As an essential nutrient, Mg²⁺ participates in the formation of chlorophyll composition. Thus, reduced uptake of Ca²⁺ and Mg²⁺ by soil salinity would have adverse effects on growth and development of cotton (Yeo. 1998). Potassium plays an important role in cotton growth, nutrient distribution and resistance to pests and diseases. Since K⁺ and Na⁺ have similar physical and chemical structure, Na⁺ can partially replace K⁺ to promote plant growth in low-K soil (Zhang et al., 2006). But at higher salt (NaCl) concentration, the selectivity of potassium for cotton plant will fall greatly. When the Na⁺ concentration exceeds a certain limit, Na⁺ will be competing with K⁺ transport and binding sites, leading to potassium depletion (Yeo, 1998). Potassium deficiency in

cotton leaves can reduce chlorophyll and photosynthesis. At the same time, excessive absorption of the Cl⁻ can reduce uptake of NO₃⁻ and H₂PO₄⁻ (Gong et al., 2009). Brugnoli and Bjorkman (1992) reported that the N content of cotton leaves decreased with increases in salt concentration. Using ¹⁵N-labeling technique, they also found that under high salinity stress, cotton plant would reduce the absorption of ¹⁵N, while at low salinity there was no significant impact on absorption (Pessarkli, 1985). Under NaCl stress, the absorption NO3-N uptake was seldom affected, but the NO₃-N accumulation was significantly decreased, and the absorption of NH₄⁺-N was greatly inhibited (Pessarkli, 2001). Using ³²P labeling technique, Martinez and Läuchli (1991) found that under low P conditions, salt stress inhibited the absorption of phosphorus in cotton seedlings. At moderate salinity, ³²P transportation from cotton root to shoot was reduced, so that old leaves of cotton contained more P than new leaves.

Control of salinity stress on cotton plants

Although cotton is classified as a salt tolerant crop, its tolerance of salinity stress is far from that of halophytes. Thus, effective management practices in combating soil salinity stress should be taken to increase cotton yield and fiber quality in saline fields. Since salinity effects on cotton are mainly attributed to osmotic stress, ion toxicity and nutritional imbalance, these effects can be alleviated through two key strategies. One is to improve salinity tolerance of cotton plants, the other is to reduce or avoid high Cl⁻ and/or Na⁺ concentration in the soil medium, at least part of the root zone. Improved salinity tolerance of cotton may be achieved through genetic improvement or enhancing the salt tolerance of seeds or plants by chemical, biological or physical treatments. A decrease in salinity stress can be achieved through the reduction of the salt content in the vadoze zone and creating a more suitable soil environment for cotton growth either with engineering or agronomic practices.

Genetic breeding

Genetic breeding, particularly molecular breeding has been considered the most efficient way to improve salinity tolerance in cotton (Gorham et al., 2009). Recently, cotton plants over-expressing TsVP [an H⁺-PPase gene cloned from Thellungiella halophila) (Lv et al., 2008)], the Arabidopsis AVP1 [a gene encoding a vacuolar pyrophosphatase as a proton pump on the vacuolar membrane (Pasapula et al., 2011)], a CMO gene cloned from Atriplex hortensis (Zhang et al., 2009), or mustard annexin AnnBj1 (Divya et al., 2010) have achieved significantly increased tolerance of salinity stress. Although molecular breeding approaches, including transgenic quantitative trait mapping and modification with marker-assisted selection, have shown some success and will continue to increase our understanding of the complexity of plant's physiological pathways (Lubbers et al., 2007), current transgenic cotton with improved salt-tolerance ability is still far behind the requirements for commercial production (Zhang et al., 2009). This is because on the one hand, the salt tolerance has not yet reached the expectation for cotton growing in saline fields, and on the other hand, strains of these salt-tolerant materials have relatively poor agronomic traits. Therefore, future studies should focus on deep exploitation of salt-tolerant genes, effective transformation and development of new salt-tolerant cotton varieties. Detailed advances in genetic breeding can be found in the previews by Lubbers et al. (2007), Gorham et al. (2009) and Ma et al. (2011).

Agents	Mode of application	Effects on stressed seeds or plants	Reference
Kinetin	Seed soaking before sowing	Alleviation of salinity effect on seed germination	Bozuck 1981
MCBuTTB	Seed soaking before sowing	Enhancement of seed	Stark 1991
(Cytokinin analog)	plus foliar spray at 45 days after planting	germination, seedling growth, and boll setting under salinity	
Polystimuline K (cytokinin analogue)	Solution culture of seedling	Leading to recovery of damaged PS II centers	Ganieva et al. 1998
Coronatine (COR)	Applied hydroponically to cotton seedlings at the two-leaf stage for 24 h.	Improving the antioxidative defense system and radical- scavenging activity	Xie et al. 2008
5-aminolevulinic acid (ALA)	Foliar spray	Improvement of salt tolerance through reduction of NaCl uptake	Watanabe et al. 2000
Gycinebetaine	Seed soaking	Allieviation of salt damage	Li et al. 2008
Calcium sulphate	Seed soaking before sowing	Enhancement of seed germination, seedling growth under salinity	Javid et al. 2001
Ca ²⁺	Applied hydroponically to cotton seedlings	Offset the reduction in root growth caused by NaCl.	Kent and Lauchli 1985
VAM (vesicular arbuscular mycorrhizal)	Mixed with soil	Increased salt tolerance of cotton seedlings	Jalaluddin 1993
Rs-5 strain (<i>Klebsiella oxytoca</i>)	Inoculation through seed soaking	Enhancement of germination and emergence under salinity stress	Yue et al. 2007
Rs-198 strain (<i>Pseudomonas</i> putida)	Inoculation through seed soaking	Protect against salt stress and promote cotton seedling growth	Yao et al. 2010

 Table 1.
 Summary of increased salt tolerance through seed soaking or foliar spray with chemical or biological agents

Chemical or biological treatment

Apart from genetic breeding, the salt tolerance of cotton plants can be improved through chemical or biological treatment. A number of chemical or biological agents have been reported to improve the salt tolerance of cotton (Table 1). Ferreira and Reboucas (1992) used pre-sowing hydration/ dehydration cycles to improve the germination of three cultivars of cotton in the presence of NaCl. In another study, pre-soaking of cotton seeds with 0.5 % solutions of CaSO₄ for 8 h prior to sowing increased the shoot and root growth (Rauf et al., 1990). Seed soaking with Ca²⁺ improved seed germination and seedling growth under salinity (Javid et al., 2001), and it offset the reduction in root growth caused by NaCl when applied hydroponically to cotton seedlings (Kent and Lauchli, 1985). Shannon and Francois (1977) found that pre-soaking of G. barbadense seeds in distilled water hastened germination. Soaking cotton seed in water for several hours before hand-sowing is used to improve germination in China, India and Pakistan, but the practice is significantly decreasing with the use of tractor-powered drills which damage the soft pre-soaked seeds (Gorham, 2009). Phytohormones or plant growth regulators have an important role in the regulation of plant metabolism by coordinating the functional activities of whole plants as well as their reaction to salinity. Bozcuk (1981) found that kinetin at 10 or 20 ppm improved the germination of cotton and alleviated the effect of salt concentrations up to 150 mM (Gorham, 2009). Foliar spray of G. barbadense cultivars with GA₃ alone or in combination with boron increased growth and monovalent cation contents under salinity, but decreased chloride content (Ibrahim, 1984). The GA₃ also alleviated the detrimental effects of salt on photosynthetic pigments in seedlings (Renu et al., 1995). Heat shock (3 h at 47°C) increased the tolerance of cotton to subsequent Na₂SO₄ salinity (Kuznetsov et al., 1990, 1993), and the response was linked to changes in the production, at different times, of ethylene, proline and putrescine (Kuznetsov et al., 1993).

Treatment (of imbibing seeds and/or as a foliar spray) with the cytokinin analog, MCBuTTB improved the germination, growth, and yield of cotton plants subjected to salinity (Stark, 1991). Another cytokinin analogue, polystimuline K, alleviated the effects of salt on photosynthetic activity in two week old cotton plants (Ganieva et al., 1998). Various treatments with PHCA (polyhydroxycarboxylic acid) have also been reported to improve yields on saline soils (Munoz, 1994). Coronatine (COR) is a chlorosis-inducing phytotoxin that mimics some biological activities of methyl jasmonate. Pretreatment with COR increased the activities of the antioxidant enzymes catalase (CAT), peroxidase (POD), and glutathione reductase (GR), and of the stable free radical, 1,1-diphenyl-2picrylhydrazyl (DPPH) in leaf tissues of salinity-stressed cotton seedlings (Xie et al., 2008). Some biological agents are able to improve the salt tolerance of cotton. Jalaluddin (1993) and Feng et al. (1999) studied the effects of salt stress on VAM (vesicular arbuscular mycorrhizal) formation and of inoculation with VAM fungi on salinity tolerance of cotton plants. They found that cotton plants inoculated with VAM had a higher biomass than non-inoculated plants. They thus suggested that the VAM fungi-plant symbiosis might play an important role in survival of plants grown on saline soils. Also, inoculation with VAM fungi could enhance crop production on saline soils and reduce yield loss due to salt stress. Yue et al. (2007) isolated the Rs-5 bacteria strain which was identified as Klebsiella oxytoca. The Rs-5 could obviously relieve salt stress and promote cotton seedling growth. Further analysis showed that it had the ability to increase cotton's absorption of N, P, K, and Ca and decrease the absorbability of Na under salt stress. In addition, Rs-5 itself could produce the phytohormone- auxin, and was capable of dissolving phosphorus. In another study, the strain, Rs-198 was isolated from an alkaline soil and identified as Pseudomonas putida on the basis of its physiological and biochemical

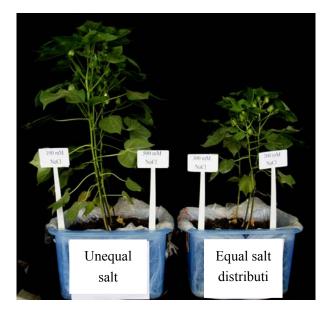


Fig 1. Improved cotton plant growth by unequal salt distribution (100/500 mM NaCl) relative to equal salt distribution (300/300 mM NaCl) in the root zone in a split-root experiment under greenhouse conditions.

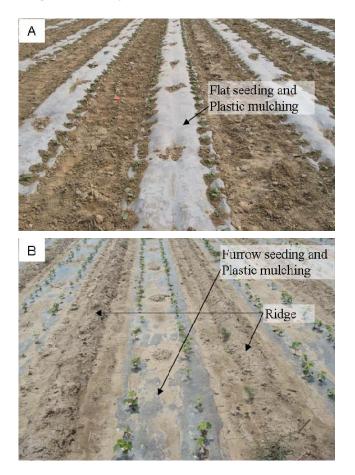


Fig 2. Cotton seedlings raised by flat seeding with plastic mulching in a moderately saline field (A) and by furrow seeding with plastic mulching in a highly saline field (B).

properties as well as its 16S rDNA sequence analysis (Yao et al., 2010). The Rs-198 could protect against salt stress and promote cotton seedling growth. The protection was attributed to increased absorption of Mg^{2+} , K^+ and Ca^{2+} , decreased uptake of Na⁺ from the soil and improved production of endogenous indole acetic acid (IAA) and reduced abscisic acid (ABA) content in salt-stressed cotton seedlings.

Mulching, furrow seeding and unequal salt distribution

Proper management of cotton with rational cultivation techniques like mulching, furrow seeding, fertilization and irrigation can alleviate salt damage to cotton plants in saline fields. Cotton plants at emergence and young seedling stages are more sensitive to salt stress than at other stages of growth in saline conditions. This explains why poor stand establishment and seedling growth are often encountered in saline soils. Because good stand establishment is a prerequisite for a bumper harvest of cotton, more attention should be paid to emergence and stand establishment during field management (Dong et al., 2008). Salinity and the related stress originate from the root-zone soil environment. Therefore, any practice that improves at least part of the root-zone environment can alleviate salt damage. The ways to improve root-zone environment include reduction of soil salinity and increases in soil moisture and temperature. In a split-root experiment, Dong et al. (2010a) confirmed that unequal salt distribution in the root-zone can alleviate salt damage to cotton plants. Potted cotton plants were grown in a split-root system in the greenhouse and each root half was irrigated with either the same or two concentrations of NaCl. When the entire root system was exposed to the same concentration of NaCl, shoot dry weight, leaf area, plant biomass, leaf chlorophyll, photosynthesis and transpiration were significantly reduced relative to the NaCl-free control (Fig. 1). Significant reductions in biological and economic yields were noticed at harvest. However, when only half of the root system was exposed to low-salinity, the inhibition effect of salinity on growth and yield was significantly reduced. Plant biomass and seed cotton yield were significantly increased compared to equal salt distribution. In another experiment, we compared cotton raised on furrow-beds in saline fields with those raised on flat beds as controls and found that furrow-bed seeding induced unequal salt distribution in saline fields (Dong et al., 2008); plant growth, yield and earliness were significantly improved. Such an improvement in yield and earliness was mainly due to unequal distribution of salts in the root zone (Fig. 2). A further study by Dong and his colleagues attributed the improvement by unequal salt distribution to increased water use, decreased Na⁺ accumulation and increased K⁺ and K⁺/Na⁺ ratio in leaves (Kong et al., 2011). Recirculation of Na⁺ from shoot to the low-salinity side of roots through the phloem is an important mechanism for reducing leaf Na⁺ accumulation in leaves. Enhanced Na⁺ efflux from the low-salinity root side induced by the high-salinity root side might also play an important role in decreasing foliar Na⁺ accumulation. The Na⁺ extrusion in salt-stressed cotton roots is mainly attributed to an active Na⁺/H⁺ antiport across the plasma membrane. Row covering with polyethylene film (plastic mulching) is a common practice in many countries because it permits early sowing with lower risk of failure. In China, this practice has become one of the most popular techniques for cotton production since the 1980s. Plastic mulching enhanced plant growth by increasing soil temperature, thus increasing cotton lint yield (Dong et al., 2007). Some other benefits of plastic mulching are increased soil temperature, water conservation, salinity control in the root zone and weed control. Plastic mulching also resulted in unequal salt distribution in the saline soil, in which part of the root system developed in relatively low-saline soil, and salt damage was thus reduced (Dong et al., 2010a; Bezborodov et al., 2010). Our further study showed that the integration of plastic mulching with furrow seeding could more effectively enhance stand establishment, earliness, yield, and yield components of cotton than mulching or furrow seeding alone (Fig 2). These improvements were due to the unequal salt distribution and elevation of soil temperature and moisture in the root-zone soon after seeding. As a result, the Na⁺ uptake by roots and leaves was reduced, peroxidation of lipids in cotton tissues was decreased, and Pn improved. The integration of plastic mulching with furrow bed seeding is a promising cotton production technique in saline areas (Dong et al., 2008; 2010a). Normal planting of full-season cotton in saline fields in temperate areas is faced with poor stand establishment, late maturity, and increasing cost of inputs. After trying late planting of short-season cotton in a saline field of the Yellow River Delta, Dong et al. (2010b) showed that late planting of short-season cotton significantly improved seed emergence and seedling growth due to increased temperature and reduced Na⁺ concentration in cotton tissues relative to normal planting. The yield from late-planted short-season cotton and normal-planted full-season cotton was comparable, but the former performed better in earliness and required less input than normal planting. Therefore, the net revenue from late-planting of short-season cotton was greater than that from normal-planting of full-season cotton. Late planting of short-season cotton is a promising system for growing cotton in saline areas of the Yellow River delta and probably in other cotton growing areas with similar ecologies (Dong et al., 2010b). Row covering is conventionally applied after sowing, but pre-sowing evaporation in spring would cause accumulation of salts and moisture loss in the surface layer of saline soils, especially in areas without pre-sowing irrigation. Row mulching with plastic film can be done 30 d before sowing (early mulching) in saline fields. Although both conventional and early mulching could effectively improve stand establishment, plant growth, earliness and lint yield of cotton, early mulching was more beneficial to stand establishment, plant growth and yield. The increased benefits of early mulching were due mainly to the better control of root-zone soil salinity, elevation of soil temperature and reduction of moisture loss. As a result, the Na⁺ accumulation in leaves and peroxidation of lipids in cotton tissues decreased, and photosynthesis improved. Mulching was more costly, but the increased yield by mulching was enough compensate for the cost increase. Early mulching is also a promising cotton production technique in the saline areas (Dong et al., 2009a).

Fertilization

Under salt stress, plant growth, nutrient absorption and metabolism, protein synthesis and water absorption are greatly altered, making it difficult for plants to fully utilize nutrients (Pessarakli, 2001; Ella and Shalaby, 1993). Therefore, proper fertilization will improve salt tolerance of cotton plants. Chen et al. (2009) studied the influence of different N fertilization rates and soil salinity levels on the growth and nitrogen uptake of cotton. They found that cotton growth was significantly affected by the interaction of soil salinity and N but not by N alone. At low to moderate soil salinity, the growth inhibition was alleviated by fertilizer application. At low to medium soil salinity, N uptake increased with N fertilization. At higher salinities, N uptake was independent of N rates and was mainly influenced by soil salinity. The uptake of K decreased with soil salinity. The concentration of Na, Cl and Ca in plant tissues increased with soil salinity with the highest concentrations in leaves. Applying nitrogen at the beginning of an irrigation cycle enhanced yield and fertilizer use efficiency (Hou et al., 2009). Jabeen and Ahmad (2009) investigated the response of cotton grown at high salinity supplemented with foliar application of KCl (500 mg/L) and NH₄NO₃ (500 mg/L) alone and in mixture. Soil salinity was maintained through irrigation with saline water. Plant growth parameters were reduced significantly at high salinity but the detrimental effects were alleviated by foliar spray of NH₄NO₃ or KCl. Foliar spray with a combination of NH₄NO₃ and KCl showed better result than spraying with either fertilizer material alone. The performance trends at the vegetative and reproductive growth stages under non-saline and saline conditions were same and varied in the order: Non-spray < water spray < KCl < NH_4NO_3 < NH_4NO_3 + KCl. Foliar nutrient spray was beneficial to both vegetative and reproductive parameters in cotton under saline environment (Jabeen and Ahmad, 2009).

Oxygation

Using aerated water for subsurface drip irrigation of crop (oxygation) might minimize the impact of salinity on plants under oxygen-limiting soil environments. Bhattarai and Midmore (2009) evaluated the effects of oxygation (12% air volume/volume of water) on cotton in a salinized vertisol at 2, 8, 14, 20 dS/m ECe. Oxygation increased lint yield and water use efficiency (WUE) by 18 and 16%, respectively and was accompanied by greater canopy light interception, plant height and stem diameter. It also enhanced photosynthesis and relative water content in the leaf, and reduced crop water stress index and leaf water potential. Oxygation improved yield and WUE of salt tolerant and moderately tolerant crops under saline soil environments, and this may have a significant impact for irrigated agriculture where saline soils are constraints to crop production (Bhattarai and Midmore, 2009).

Conclusion

Salt damage to cotton plants in saline soils is mainly due to ion toxicity, osmotic stress and nutrient imbalance. The external manifestations of salt damage are usually the inhibition of seed germination, emergence and seedling growth, reduced biomass and economic yield, etc., while the internal effects are mainly the physiological and biochemical changes. Both internal and external symptoms of salt damage depend on level and longevity of salt stress, and vary with growth stages. Cotton plants at emergence and young seedling stages are more sensitive to salt stress than at other stages, thus more attention should be paid to stand establishment, especially at the seedling stage when growing cotton on a saline soil. Increasing salt tolerance of cotton and high Cl⁻ and/or Na⁺ concentration in the soil medium are two effective strategies for controlling salt damage to cotton. Currently, several ways or practices for improving the salt tolerance of cotton have been determined. Although some progress in salt-tolerant improvement of cotton has been made, particularly through molecular breeding, the development of salt-tolerant cotton is not an easy job due to the complexity of the tolerance mechanisms, narrow germplasm resource, lack of selection criteria and variation in salt responses at different developmental stages (Ashraf et al., 2008). Seed or plant treatment with chemical or biological agents is also an effective alternative in improving salt tolerance in cotton. There are also a number of agronomic practices which can effectively control salt damage through improvement in root-zone soil environment. Plastic mulching, furrow seeding, late-planting of short season-cotton, irrigation and fertilization either reduced salinity, increased temperature and moisture, or increased supply of nutrients in the soil root-zone, thus reducing the salt damage in saline fields. However, all the practices have their own limitations (Qadir et al. 2000). From the present point of view, a more realistic approach is to adopt comprehensive practices, including saline soil improvement through agronomic and engineering practices, application of salt-tolerant cultivar, seed and plant treatment, specific planting like mulching and furrow seeding, proper fertilization and other agronomic practices. Further research should focus on the following three aspects: The first is to develop specific cotton cultivars with high salt tolerance through a combination of traditional breeding methods and molecular technologies. The second is to further explore and understand the supply and uptake characteristics of water and fertilizer, and to explore new alternatives to improve uptake and use efficiency of nutrients and water in saline soils. The third is to develop new products for cotton growing in saline soils, including new foliage fertilizer, specific slow-released fertilizer and commercial plant growth regulators.

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References

- Ahmad S, Khan N, Iqbal MZ, Hussain A, Hassan A (2002) Salt tolerance of cotton (*Gossypium hirsutum* L.). Asian J Plant Sci 1: 715–719.
- Apse MP, Aharon GS, Snedden WA, Blumwald E (1999) Salt tolerance conferred by overexpression of a vacuolar N+/H+ antiport in Arabidopsis. Science 285: 1256–1258.
- Ashraf M (1994) Breeding for salinity tolerance in plants. Crit Rev Plant Sci 13: 17–42.
- Ashraf M (2002) Salt tolerance of cotton: some new advances. Crit Rev Plant Sci 21: 1–30.
- Ashraf M, Athar HR, Harris PJ, Kwon TR (2008) Some prospective strategies for improving crop salt tolerance. Adv Agron 97: 45–110.
- Bezborodov GA, Shadmanov DK, Mirhashimov RT, Yuldashev T, Qureshi AS, Noble AD, Qadir M (2010) Mulching and water quality effects on soil salinity and sodicity dynamics and cotton productivity in Central Asia. Agri Ecosyst Environ 138: 95–102.
- Bhattarai SP, Midmore DJ (2009) Oxygation enhances growth, gas exchange and salt tolerance of vegetable soybean and cotton in a saline vertisol. J Integr Plant Bio 51: 675–688
- Booth WA, Beardall J (1991) Effect of salinity on inorganic carbon utilization and carbonic anhydrase activity in the halotolerant algae *Dunaliella salina* (Chlorophyta). Phycologia 30: 220–225.
- Bozuck Bozcuk S (1981) Effects of kinetin and salinity on germination of tomato, barley and cotton seeds. Ann Bot 48: 81–84.
- Brugnoli, Bjorkman OE (1992) Growth of cotton under continuous salinity stress: influence on allocation pattern, stomatal and non-stomatal components of photosynthesis and dissipation of excess light energy. Planta 187: 335–347.

- Chaves MM, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot 103: 551–560.
- Chen W, Hou Z, Wu L, Liang Y, Wei C (2010) Effects of salinity and nitrogen on cotton growth in arid environment. Plant Soil 326: 61–73.
- Cramer GR (1987) Influx of Na⁺, K⁺, Ca²⁺ into roots of salt-stressed cotton seedling. Plant Physiol 83: 510–516.
- Divya K, Jami S K, Kirti P B (2010) Constitutive expression of mustard annexin, AnnBj1 enhances abiotic stress tolerance and fiber quality in cotton under stress Plant Mol Biol 73: 293–308.
- Dong H, Kong X, Luo Z, Li W, Xin C (2010a) Unequal salt distribution in the root zone increases growth and yield of cotton. Eur J Agron 33: 285–292.
- Dong H, Li W, Tang W, Li Z, Zhang D (2007) Enhanced plant growth, development and fiber yield of Bt transgenic cotton by an integration of plastic mulching and seedling transplanting. Ind Crop Prod 26: 298–306.
- Dong H, Li W, Tang W, Zhang D (2008) Furrow seeding with plastic mulching increases stand establishment and lint yield of cotton in a saline field. Agron J 100: 1640–1646.
- Dong H, Li W, Tang W, Zhang D (2009a) Early plastic mulching increases stand establishment and lint yield of cotton in saline fields. Field Crop Res 111: 269–275.
- Dong H, Li W, Xin C, Tang W, Zhang D (2010b) Late-planting of short-season cotton in saline fields of the Yellow River Delta. Crop Sci 50: 292–300.
- Dong H, Xin C, Li W (2009b) Characteristics of salinity and fertility in coastal saline cotton fields in Shandong and their effects on cotton emergence. Cotton Sci 21: 290–295.
- Ella MKA, Shalaby ES (1993) Cotton response to salinity and different potassium-sodium ratio in irrigation water. J Agron Crop Sci 170: 25–31.
- Feng G, Bai D, Yang M, Li X, Zhang F (1999) Effect of salinity on VA mycorrhiza formation and of inoculation with VAM fungi on saline-tolerance of plants. Chin J Appl Ecol 10: 79–82.
- Ferreira LGR, Reboucas MAA (1992) Influence of hydration dehydration on cotton seeds on overcoming the effects of salinity on germination. Pesquisa Agropecuaria Brasileira 27: 609–615.
- Flowers TJ, Hajibagheri MA, Yeo AR (1991) Ion accumulation in the cell walls of rice plants growing under saline conditions: evidence for the Oertli hypothesis. Plant Cell Environ 14: 319–325.
- Ganieva RA, Allahverdiyev SR, Guseinova NB, Kavakli HI, Nafisi S (1998) Effect of salt stress and synthetic hormone polystimuline K on the photosynthetic activity of cotton (*Gossypium hirsutum*). Tr J Bot 22: 217–221.
- Gong J, Lu N, Ru S, Hou Z (2009) Effects of soil salinity on nutrients and ions uptake in cotton with drip irrigation under film. Acta Metallurgica Sinica 15: 670–676.
- Gorham J, Lauchli A, Leidi E O (2009) Plant responses to salinity. pp. 130-142. In: J.M. Stewart, D.M. Oosterhuis, J.J. Heitholt, J.R. Mauney (eds.). Physiology of Cotton. National Cotton Council of America, Memphis, Tenn. Springer, London.
- Gouia H, Ghorbal MH, Touraine B (1994) Effects of NaCI on flows of N and mineral ions and on NO₃-reduction rate within whole plants of salt-sensitive bean and salt-tolerant cotton. Plant Physiol 105: 1409–1418.
- Greenway H, Munns R (1980) Mechanisms of salt tolerance in non halophytes. Ann Rev Plant Physiol 31: 149–190.
- Haque SA (2006) Salinity problems and crop production in coastal regions of Bangladesh. Pak J Bot 38(5): 1359–1365.

- He C, Shen G, Pasapula V, Luo J, Venkataramani S, Qiu X, Kuppu S, Kornyeyev D, Holaday A S, Auld D, Blumwald E, Zhang H (2007) Ectopic expression of AtNHX1 in cotton (Gossypium hirsutum L.) increase proline content and enhances photosynthesis under salt stress conditions. J. Cotton Sci 11: 266–274.
- He C, Yan J, Shen G, Fu L, Holaday AS, Auld D, Blumwald E, Zhang H (2005) Expression of an Arabidopsis vacuolar sodium/proton antiporter gene in cotton improves photosynthetic performance under salt conditions and increases fiber yield in the field. Plant Cell Physiol 46: 1848–1854
- Higbie S M, Wang F, Stewart J McD, Sterling TM, Lindemann WC, Hughs E, Zhang J (2010) Physiological response to salt (NaCl) stress in selected cultivated tetraploid cottons. Int J Agron 1: 1–12.
- Hirayama O (1987) Characterization of membrane lipids of high plants, different in salt tolerance. Agri Biol Chem 51: 3215–3321.
- Hou Z, Chen W, Li X, Xiu L, Wu L (2009) Effects of salinity and fertigation practice on cotton yield and ¹⁵N recovery. Agr Water Manage 96: 1483–1489
- Ibrahim AA (1984) Effect of GA3 and boron on growth, yield and accumulation of Na, K, and Cl in cotton grown under saline conditions. Ann Agric Sci Moshtohor 21: 519–531.
- Jabeen R, Ahmad R (2009) Alleviation of the adverse effects of salt stress by foliar application of sodium antagonistic essential minerals of cotton (*Gossypium hirsutum* L). Pak J Bot 41: 2199–2208.
- Jalaluddin M (1993) Effect of VAM fungus (*Glomus intradices*) on the growth of sorgum, maize, cotton and pennisetum under salt stress. Pak J Bot 25: 215–218.
- Javid A, Yasin M, Nabi G (2001) Effect of seed pre-treatments on germination and growth of cotton (*Gossypium hirsutum* L.) under saline conditions. Pak J Biol Sci 4: 1108–1110.
- Karimi G, Ghorbanli M, Heidari H, Khavarinejad RA, Assareh MH (2005) The effects of NaCl on growth, water relations, osmolytes and ion content in Kochia prostrate. Biol Plant 49: 301–304.
- Kent LM, Läuchli A (1985) Germination and seedling growth of cotton: Salinity-calcium interactions. Plant Cell Environ 8: 155–159.
- Khan AN, Qureshi RH, Ahmad N (1995) Selection of cotton cultivars for salinity tolerance at seedling stage. Sarhad J Agric 1: 153–159.
- Khan AN, Qureshi RH, Ahmad N (2004) Effect of external sodium chloride salinity on ionic composition of leaves of cotton cultivars II. cell sap, chloride and osmotic pressure. Int J Agric Biol 6: 784–785.
- Khorsandi F, Anagholi 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, Dong H, Eneji AE, Li W (2011) Effects of non-uniform root zone salinity on water use, Na⁺ recirculation, and Na⁺ and H⁺ flux in cotton. J Exp Bot doi:10.1093/jxb/err420
- Kuznetsov VV, Khydyrov BT, Roschupkin BV, Borisova NN (1990) Common systems of resistance to salinity and high temperature in cotton facts and hypotheses. Soviet Plant Physiol 37: 744–752.
- Kuznetsov VV, Rakitin VU, Borisova NN, Roshchupkin BV (1993) Why does heat shock increase salt resistance in cotton plants. Plant Physiol Biochem 31: 181–188.

- Li Y, Song X, Yang X (2008) Effects of seed soaking with glycinebetaine on the salt tolerance of cotton seedlings. Acta Agron. Sin. 34: 305–310.
- Lin H, Salus SS, Schumaker KS (1997) Salt sensitivity and the activities of the H⁺-ATPases in cotton seedlings. Crop Sci 37: 190–197.
- Lobell DB, Ortiz-Monsterio JI, Gurrola FC, Valenzuuela L (2007) Identification of saline soils with multiyear remote sensing of crop yields. Soil Sci Soc Am J 71: 777–783.
- Lubbers EL, Chee PW, Saranga Y, Paterson AH (2007) Recent advances and future prospective in molecular breeding of cotton for drought and salinity stress tolerance. In: Advances in Molecular Breeding Towards Drought and Salt Tolerant Crops. pp775–796. (Eds.): Jenks MA, Hasegawa PM, Jain SM. Springer, The Netherlands.
- Luo Q, Yu B, Liu Y (2002) Stress of Cl⁻ is stronger than that of Na⁺ on glycinemax seedling under NaCl stress. Agri Sci China 1: 1404–1409.
- Lv S, Zhang K, Gao Q, Lian L, Song Y., Zhang J (2008) Overexpression of an H⁺-PPase gene from Thellungiella halophila in cotton enhances salt tolerance and improves growth and photosynthetic performance. Plant Cell Physiol 49: 1–15.
- Ma X, Dong H, Li W (2011) Genetic improvement of cotton tolerance to salinity stress. Afr J Agric Sci 6: 6797-6803.
- Maas EV (1990) Crop salt tolerance. In: Tanji KJ (ed.). Agricultural Salinity Assessment and Management. American Society of Civil Engineers, New York. pp. 262–304.
- Maas EV, Grattan SR (1999) Crop yields as affected by salinity. In: Skaggs RW, van Schilfgaarde J (eds) Agricultural Drainage, Agron Monogr 38. ASA, CSSA, SSA, Madison, WI, pp 55–108.
- Maas EV, Hoffman GJ (1977) Crop salt tolerance—current assessment. J Irrig Drain Div Am Soc Civ Eng 103: 115–134.
- Martinez V, Läuchli A (1991) Phosphorus translocation in salt-stressed cotton. Physiol Plantarum 83, 627–632.
- Meloni DA, Oliva MA, Martinez CA, Cambraia J (2003) Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. Environ Exp Bot 49: 69–76.
- Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25: 239–250.
- Munns R (2005) Genes and salt tolerance: bringing them together. New Phytol 167: 645–663.
- Munns R, Tester M (2008). Mechanisms of salinity tolerance. Annu Rev Plant Biol 2008. 59: 651–81.
- Munoz SC (1994) Nutrient uptake and plant physiology enhancement by PHCA treatments on cotton plants. pp. 1360–1363 In: 1994 Proc. Beltwide Cotton Conferences, National Cotton Council of America, Memphis, Tenn.
- Nawaz K, Hussain K, Majeed A, Khan F, Afghan S, Ali K (2010) Fatality of salt stress to plants: Morphological, physiological and biochemical aspects. Afr J Biotech 9(34): 5475–5480.
- Pasapula V, Shen G, Kuppu S, Paez-Valencia J, Mendoza M, Hou P, Chen J, Qiu X, Zhu L, Zhang X, Auld D, Blumwald E, Zhang H, Gaxiola R, Payton P (2011) Expression of an Arabidopsis vacuolar H+-pyrophosphatase gene (AVP1) in cotton improves drought- and salt tolerance and increases fiber yield in the field conditions. Plant Biotechnol J 9: 88–99
- Pessarakli M (2001) Physiological responses of Cotton (*Gossypium hirsutum* L.) to salt stress. In: Handbook of plant and Crop Physiology. (Ed.): M. Pessarakli. Marcel Dekker, New York, pp.681–696.

- Pessarakli M, Tucker T C (1985) Uptake of ¹⁵N by cotton under salt stress. J Soil Sci Soc Am 49: 149–152.
- Praharaj CS, Rajendran TP (2004) Soil salinity management in cotton.

http://www.thehindu.com/thehindu/seta/2004/03/18/stories/2 004031800411700.htm

- Pritchard J, Jones RG W, Tomos AD (1991) Turgor, growth and rheological gradients of wheat roots following osmotic stress. J Exp Bot 42: 1043-1049.
- Qadir M, Ghafood A, Murtaz AG (2000) Amelioration strategies for saline soils: A review. Land Degrad, Develop. 11: 501–521.
- Qadir M, Shams M (1997) Some agronomic and physiological aspects of salt tolerance in cotton (*Gossypium hirsutum* L.). J Agron Crop Sci 179: 101–106.
- Rathert G (1982) Influence of extreme K/Na ratios and high substrate salinity on plant metabolism of crops differing in salt tolerance. Mineral distribution variability among different salt tolerant cotton varieties. J Plant Nutr 5: 183–194.
- Rauf A, Razzaq A, Muhammad S, Akhtar J (1990) Improvement in salt tolerance of cotton. Pak J Agric Sci 27: 193–197.
- Renu M, Goswami CL, Munjal R (1995) Response of chloroplastic pigments to NaCl and GA3 during cotton cotyledonary leaf growth and maturity. Agric Sci Digest Karnal 15: 146–150.
- Richards LA (ed.) (1954) Diagnosis and improvements of saline and alkali soils. USDA. Agriculture Handbook 60. p160.
- Shannon MC, Francois LE (1977) Influence of seed pretreatments on salt tolerance of cotton during germination. Agron J 69: 619–622.

- Stark C (1991) Osmotic adjustment and growth of salt-stressed cotton as improved by a bioregulator. J Agron Crop Sci 167: 326–334.
- Tang W, Luo Z, Wen S, Dong H, Xin C, Li W (2007) Comparison of inhibitory effects on leaf photosynthesis in cotton seedlings between drought and salinity stress. Cotton Sci 19: 28–32.
- Tavakkoli E, Rengasamy P, McDonald GK (2010) High concentrations of Na⁺ and Cl⁻ ions in soil solution have simultaneous detrimental effects on growth of faba bean under salinity stress. J Exp Bot 61: 4449–4459.
- Watanabe K, Tanaka T, Hotta Y, Kuramochi H, Takeuchi Y (2000) Improving salt tolerance of cotton seedlings with 5-aminolevulinic acid. Plant Grow Regul 32: 99–103.
- Xie Z, Duan L, Tian X, Wang B, Eneji AE, Li Z (2008) Coronatine alleviates salinity stress in cotton by improving the antioxidative defense system and radical-scavenging activity. J Plant Physiol 165: 375–384.
- Yao K, Wu Z, Zheng Y, Kaleem I, Li C (2010) Growth promotion and protection against salt stress by Pseudomonas putida Rs-198 on cotton. Eur J Soil Biol 46: 49–54
- Yeo A (1998) Molecular biology of salt tolerance in the context of whole plant physiology. J Exp Bot 49: 915–929.
- Yue HT, Mo WP, Li C, Zheng YY, Li H (2007) The salt stress relief and growth promotion effect of Rs-5 on cotton. Plant Soil 297: 139–145.
- 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. Breeding 23: 289–298.
- Zhang Y, Li Q, Zhou X, Zhai C, Li R (2006) Effects of partial replacement of potassium by sodium on cotton seedling development and yield. J Plant Nutr 29: 1845–1854.