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Salinity Stress in Cotton: Adverse Effects, Survival Mechanisms and Management Strategies

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4.1 Introduction

Globally, abiotic stresses such as drought, salinity, heat, soil erosion, waterlogging, heavy metals toxicity, etc. are posing serious challenges to modern farming systems under the changing climate (Iqbal 2020; Iqbal et al. 2015; Iqbal and Iqbal 2015; Raza et al. 2019; EL Sabagh et al. 2020). Among abiotic stresses, salinity is a global problem and is mostly found in arid and semi-arid regions due to the accumulation of free salt (Hussain et al. 2019a; Bange et al. 2004; EL Sabagh et al. 2020b; Hafeez et al. 2021; Hossain et al. 2020a, 2020b; Tariq et al. 2013). Around 6% of the total land area of Asia, the Pacific, and Australia is severely affected by salinity. Soil salinity is the single most pertinent factor, restraining about 20% of agricultural productivity of the cultivated area and one-half of the irrigated area throughout the world (Machado and Serralheiro 2017). Saline soils are defined in terms of electrical conductivity (EC) of saturated paste extract with soils whose EC is greater than 4 dS m^{-1} at 25°C (Simões et al. 2016; Abrol et al. 1988). Various crops respond differently to salinity threshold levels (Table 4.1).

Cotton (*Gossypium hirsutum* L.) is tolerant to soil salinity with a threshold level of 7.7 dS m^{-1} (Zhang et al. 2013; Hou et al. 2009; Gillham et al. 1995; Lu and Zeiger 1994) and thus can give reasonable productivity if grown on saline soil and will eventually result in economic development in high salinity regions. Cotton is a natural fibre crop used globally as fuel, edible oil, and manufacturing garments (Gormus et al. 2017a, 2017b; Omar et al. 2018; Ahmad et al. 2018; Han and Kang 2001). During its life cycle, it faces numerous biotic as well as abiotic stresses, and sustainable cotton production is severely affected due to salt stress. Stages of cotton crop vary in their capability to stand different salt stress levels (Santhosh and Yohan 2019). Due to saline conditions, salt stress at the cellular level interrupts the osmotic, as well as ionic homoeostasis, constrains photosynthesis, and decreases the cellular energy, which ultimately leads to redox imbalance (Gupta et al. 2020). Stress due to soil salinity constrains plant growth, primarily by inhibiting leaf expansion and reducing net photosynthetic rate (Pn). This reduced Pn is primarily due to stomatal closure or feedback from

TABLE 4.1

An overview of Important Crops Regarding Their Salt Tolerance Ability

Crops	The Threshold Level of EC (dSm^{-1})	Status of Crop	Sensitive Stages	Yield Loss due to Salt Stress (%)	References
Cotton	7.7	Tolerant	Germination, emergence of first reproductive branches	50–90	Zhang et al. 2013
Wheat	6	Moderately tolerant	Tillering, plume formation, head, and grain formation	13.4	Mojid and Wyseure (2013)
Sorghum	2.8	Moderately sensitive	Emergence, flowering, and soft dough stages throughout the growing season	50	Banerjee and Roychoudhury (2018)
Rice	2	Moderately Sensitive	Tillering, plume formation, head, and grain formation	30–35	
Sugarcane	1.7	Moderately sensitive	Vegetative growth and sucrose formation	10–100	Simões et al. (2016)
Maize	1.3	Moderately sensitive	Earlier vegetative growth stages	16–22	Katerji et al. (2000)
Onion	1.21	Sensitive	Seedling, vegetative growth, bulb size, and bulb diameter	50	Sta-Baba et al. (2010)

enhanced sucrose levels in source leaves. Salt stress adversely influences cotton physiology from germination to boll development, emergence rate, plant height, and leaf number. Subsequently, reduced photosynthesis affects the metabolism activity of the cell and eventually results in irregular growth of the plant (Zhang et al. 2016).

The current study intends to synthesize numerous adverse effects of salinity on the growth, lint production, and fibre quality parameters of cotton. In addition, the tolerance mechanism to cope with the saline environment has been objectively highlighted. Moreover, various management approaches for boosting lint yield and fibre quality by ameliorating the adverse effects of salinity stress have also been critically assessed.

4.2 Morpho-physiological Mechanisms of Cotton in Response to Abiotic Stresses

4.2.1 Effect of Abiotic Stresses on Cotton

Cotton crop is sensitive to abiotic stresses like drought, temperature, and salinity, especially the incidence of abiotic stresses at the reproductive stage leading to senescence of flowers and ultimately lowering lint yield. Among various effects of abiotic stresses on reproductive parts, spike denaturing is the most common effect caused by ethylene toxicity. It is important to prevent senescence of reproductive parts due to this ethylene toxicity. Using ethylene inhibitor is the best technique to prevent this loss of reproductive parts (Costa and Azevedo 2010).

4.2.2 Effect of Drought Stress on Cotton Yield

Moisture deficit condition is one of the imperative abiotic stresses, which causes a severe decline in crop production potential (EL Sabagh et al. 2020b). Limited soil moisture contents reduce plant capability towards yield and inhibit plant intercellular activities (Muller et al. 2011; Carmo-Silva et al. 2012; Raza et al. 2020). Therefore, drought stress is considered the main stress among abiotic stresses that hampers plant yield and quality (Basal et al. 2009; Schittenhelm 2010). Cotton is an imperative crop susceptible to water shortage (Loka 2012). In many cotton developing areas, moisture deficiency is frequently implemented at the boll formation stage. Cotton is more susceptible to drought stress at the boll formation phase than other phases (Loka and Oosterhuis 2012). Duration and intensity of moisture stress depend on the weather forecast (Giorgi and Lionello 2008). For making sure the long-time spam of cotton production, it is necessary to know better about the consequences of moisture stress on reproductive growth, yield, and fibre quality. Many researchers have explored adverse effects of moisture stress on yield and fibre quality of cotton, whereby reproductive growth of cotton was especially prone to salinity (Rontain et al. 2002; Basal et al. 2009; Lokhande and Reddy 2014). Water stress can lower the boll formation and boll weight with the aid of using various levels of field capacity (Basal et al. 2009; Lokhande and Reddy 2014). The increase and reduction in various yield-related traits are associated with moisture deficiency (Snowden et al. 2013; Rahman et al. 2018).

It is pertinent to mention that all yield-related traits of crops, including cotton, are not equally affected by suboptimal moisture conditions. Lint yield is the main plant character that is reduced under moisture deficit stress, and it usually depends upon the condition of distinctive fruit branches. Boll biomass distribution and seed number per boll on upper fruiting branches are also altered by moisture deficit stress. Fibre length and quality are declined with the decrease in water availability at better fruiting branches. Under identical moisture conditions, the micronaire efficiency at better fruiting branches is better, and drought has no lasting impact on the micronaire efficiency (Wang et al. 2016; Rahman et al. 2019; Rahman et al. 2016a).

4.2.3 Effect of Salt Stress on Cotton Yield

Salt toxicity negatively impacts the physiology from germination to boll development, which properly explains the resistance mechanism (Manikandan et al. 2019; Hafeez et al. 2021). It has been verified that germination rate, plant canopy, and leaves density are the high-quality morphological signs for pointing out salt tolerance. Cotton is highly vulnerable to yield reduction up to 30% in salt-affected soils (Ouda et al. 2014). After the threshold salinity of 7.7 dS m^{-1} in *Gossypium hirsutum,* every 1 dS m^{-1} increase in EC decreased the yield up to 5.2% (Maas 1990). Cotton yield decline under saline conditions was related to fluctuations in dissolved salts in soil solution (Ahmad et al. 2002) and plant leaves (Zhang et al. 2014). A comparable yield reduction is found in fields irrigated with saline water. Cotton yields have reduced by using 9% gypsum because of alternate weather in saline areas. It has been found that cotton yield decreases by 10–20% at EC value of 5 dS m^{-1} and by 27% at 8 dS $m^{-1.}$ (Hebbar et al. 2005). Although the plant is classed as salt-tolerant, this tolerance is not limited; however, it varies with the advancement in growth stages of the plant (Qidar and Shams 1997). Several types of experiments had been carried out to assess the impact of salinity on germination, vegetative growth cycle, and yield of cotton (Guo et al. 2012).

4.2.4 Effect of Heat Stress on Cotton Yield

The temperature necessities of cotton species range from the phenological duration of the genus. This distinction can extrude now no longer simplest with the phenological duration, however additionally with the time spam of temperature, physiological morphology and genetic shape of the plant. Many studies describe the temperature effects on cotton yield (Burke and Wanjura 2009). Cotton is a plant that can tolerate a hot climate; however, an increase in temperature above optimum hampers cotton productivity (Oosterhuis 2002; Rahman et al. 2018). Heat stress reduces the growth period of cotton, which badly impacts many agronomic and morphological characteristics of cotton such as sympodial branches, monopodial branches, seed numbers per boll, lint yield, and fibre quality (Khan et al. 2008; Rahman et al. 2016b), especially for economically important genotypes (Lu and Zeiger 1994). The improvement in growth characteristics of cotton plants, inclusive of shoot development, flowering, and fibre quality, is significantly declined by excessive temperature (Noshair Khan et al. 2014; Saifullah et al. 2015; Farooq et al. 2015; Wajid et al. 2014). Plant height is significantly increased by heat stress (Pace et al. 1999).

Plant size, sympodial branches can maintain the first position in the field due to high-temperature stress decreases under controlled conditions (Zeeshan et al. 2010; Akhtar et al. 2013). Heat stress reduces pollination (Burke et al. 2004) and subsequent fertilization, resulting in fewer seeds per ball (Snider et al. 2010). Oosterhuis (1999) has described an adverse relation between yield and heat stress during boll formation. Heat stress being associated with low yield, the seeds per boll, boll retention rate (Maggio et al. 2000), and high temperature decreased the fruiting rate and number of nodes (Akhtar et al. 2013). Earlier research suggested that warm temperature declined the initiation of flowers (Saifullah et al. 2015; Farooq et al. 2015). Noshair Khan et al. (2014) found that heat stress also reduced the shoot density and flower initiation in cotton crops.

4.2.5 Effect of Heavy Metals on Cotton Yield

Heavy metals such as cadmium (Cd), copper (Cu), lead (Pb), and zinc (Zn) have numerous negative effects on plant growth, cottonseed yield, and fibre quality (Wang et al. 2007). Very few studies have been conducted to assess the impact of heavy metals toxicity on cotton. In contrast, Cd, which is a non-essential element, is highly toxic to cotton plants. It is absorbed by roots, transported across plant tissues, and finally gets accumulated in roots, buds, fruits, and grains (Qian et al. 2009). The adverse results of Cd on plant life can be associated with the interference of Cd with numerous metabolic processes (Li et al. 2012). A massive variety of studies suggested that immoderate cadmium in plant life can cause plant growth retardation, chlorosis, leaf shrinkage, and necrosis (Khan et al. 2016; Xue et al. 2013).

4.2.6 Effect of Light/Radiation Intensity on Cotton Growth and Yield

Light is the primary restricting factor in cotton production. Although the impact of shading on cotton yield has been verified in several studies, light intensity in field-grown cotton causes disturbance in physiological mechanisms, which ultimately causes boll shading. Due to the uncertainty of cotton plant growing patterns, the results of mild low pressure at exceptional levels increase cotton yield (Zhao and Oosterhuis 1998). Of the various electromagnetic radiation spectra (ERS) that reach the Earth's atmosphere, the human eye can best stumble on a small part of this spectrum. This component intently corresponds to the photosynthetic radiation, and with its range of 400–700, photosynthetically active radiation is reasonable for the photosynthetic efficiency and electron transport response in plants and the long-run increase in plant yields. However, radiation other than this range additionally influences the body structure of vegetation. Infrared and purple radiation may be detected with plant pigments (a blue pigment). Photomorphogenesis refers back to the plant pigments, crypto-chromes, and phototrophic proteins in vegetation that increase with mild changes. Ultraviolet rays have a terrible effect on plant growth and yield.

Insufficient light will decrease the intensity of electrons released during photosynthetic activity, as well as a hydrolytic activity, during the photosynthetic process and finally decrease cotton yield. More light intensity may be the reason for photo-inhibition, a photo-damaging responsive mechanism that will also decrease plant yield. Changes in light intensity affect the growth and transpiration rate of *Gossypium hirsutum* plants, and chlorophyll contents are highly susceptible to light intensity. Low light intensity has adverse effects on the growth and yield of cotton, and the lack of light leads to stunt growth (Santosh and Yohan 2019).

Studies have indicated that early growth stages like germination, emergence, and seedling are more affected by salinity compared to later growth stages of cotton. Salinity causes late flowering, fewer fruits set, loss of fruit, and a decreased bulb weight, which eventually affects the yield of seed cotton. It suppressed metabolic enzyme activities, namely: Acidic invertase, alkaline invertase, and sucrose phosphate synthase leading to the deterioration of the salt content of the fibre quality. The detail is shown in the following lines.

4.2.6.1 Germination

Seedlings are greater prone to salinity than the juvenile phase. In the cotton crop, a severe drop in germination percentage was found above 10 dSm^{-1}. Due to salt stress, cotton sprouting, as well as emergence phases, is severely delayed. At 15–20 dSm^{-1}, the emergence of the plant was observed to delay by 4–5 days as compared to a plant grown under normal conditions; because of poor germination, the plant population decreases, resulting in an overall reduction in cotton yield (Sharif et al. 2019). At the germination stage, salt tolerance can be estimated by analyzing germination potential, germination rate, fresh mass, and vigour index. High salinity affects the cell wall and membrane permeability and inhibits the imbibition of water and other ions. Seed germination is a good indicator of salt tolerance in cotton; however, using germination percentage as a sole indicator of salinity tolerance could be misleading.

4.2.6.2 Growth

Salinity significantly affects root morphology and root growth. However, soil salinity was reported to bring change in root characteristics, such as orientation (anisotropy), development of root cell pattern, cell elongation rate, root length, root density, and shape. Salinity stress inhibits the cotton tissue development pattern at the root tip and stimulates the root endodermis and exodermis with delayed primary root growth and poor lateral roots. According to Soares et al. (2018), irrigation with saline water at the vegetative and reproductive phases can be utilized in cotton cultivation with minimum losses in growth, biomass buildup, and fibre quality.

4.2.6.3 Root Growth

Soil salinity normally results in decreased root length, and the secondary roots are also affected, contributing to reduced growth of roots. As the magnitude of salinity in soil increases, there is a gradual decrease in primary roots' growth while the length of secondary roots starts to decrease at mild salt stress. The ionic influx in the roots and its movement toward the shoot is mainly responsible for developing plants. Comparatively decreased sodium ion retention in the roots results in lower root growth than shoot.

4.2.6.4 Shoot Growth

Research on cotton and salt stress confirms that cotton can withstand salt stress, but too much salt will negatively affect yield. However, some researchers have also observed the improvement of plants due to a reduction in salt pressure. This may be due to the sparing effect of nutrients or due to the presence of micronutrients as impurities in the saline growth medium. Salinity reduces the shoot/root ratio, as observed by Babu et al. (1987). Khan et al. (1998b) studied the behaviour of cotton types D-9, MNH-93, NIAB-78, and Ravi under different salt solutions. They found that salt stress-induced by NaCl slowed down bud growth, and the effect of salt stress can be ameliorated by adding Ca^{2+} to the rooting medium. It was found that NIAB-78 was more salt-tolerant among all the strains. This information shows that cotton cultivation is highly dependent on salt stress conditions, but different genetic lines respond differently to salt stress.

4.2.7 Cotton Boll Development and Yield

Cotton bolls and boll size are premier yield contributing parameters. The diminished number of boll and boll size due to the expansion of soil saltiness basically reduces cotton crop yield. The overdue flowering is primarily due to the effect of salt stress in the vegetative growth stage. In cotton, 60–87% synthesized sucrose is transported from subtending leaf of cotton boll (SLCB) to developing bolls, and it plays a prominent role in cotton yield. Under saline conditions, sucrose accumulation in SLCB is not affected, but its efficient transportation towards developing bolls is retarded, resulting in reduced boll weight (Peng et al. 2016a; Rahman et al. 2016b). Cotton crop outcome was decreased to 50% at 17 dS m^{-1}; however, lower levels of salinity had no negative consequence on crop development. On the other hand, early leaf agedness and shedding occurred with the upsurge in the soil salinity. It was observed that irrigation containing high salt concentration in the cotton crop at the budding stage reduced the overall cotton yield up to 90% and declined the cotton fibres' quality during bulb development (Soares et al. 2018).

4.2.8 Fibre Quality

Fibre quality is a hereditary characteristic that is also influenced by an adverse environment. Salinity reduces fibre length, quality, and development while enhances fibre fineness. Fibre length and quality are diminished with the increasing levels of sodium ions. Processes like cellulose deposition, photosynthesis process, and sugar transport are affected by higher EC values, ultimately affecting fibre maturity. Decreased mature fibre is produced due to decreased cross-sectional area, which is a consequence of lower cellulose deposition. Cellulose deposition is responsible for fibre quality, while the metabolism of sucrose is responsible for cellulose synthesis. More than 85% of the cellulose is present in the mature fibre. The synthesis and buildup of mature fibre occur during the thickening of fibre, and next to fibre elongation, its deposition begins due to an upsurge in cellulose synthesis. Cellulose content and sucrose transformation rate are diminished as salt stress increases. In saline conditions, sucrose is available, but cellulose conversion is inhibited due to suppressed processes of metabolic enzymes such as acidic invertase, phosphate synthase and alkaline invertase. Saline water irrigation during boll development results in poor quality cotton. Salt sensitive cultivars show high Cl^{-} in leaves and get poor quality fibre. Salt tolerant cultivars accumulate high K^{+} and Ca^{2+} in leaves. High soil salinity increases the ginning out-turn and micronaire, decreasing the staple length, fibre maturity, and fibre strength. It confirms that salt tolerance is associated with nutrient accumulation in plant tissues. Under salinity, poor fibre quality is obtained, and it may be due to the decreased maturity of individual fibres. Higher salinity decreased fibre length, fibre strength, and fineness. Internationally the main purpose of cotton breeding and its various genetic programs is to improve fibre quality. A summary of the effects of salinity on various growing phases of cotton is shown in Table 4.2.

TABLE 4.2

Effect of Salinity on Various Cotton Growth Stages

Growth Stages	Causes	Effect on Growth	References
Germination	Less and delayed germination due to reduced germination potential, vigour index and fresh mass.	Negative	(Guo-Wei et al. 2011)
Emergence	Delayed emergence results in the non-availability of nutrients. Less plant vigour results in poor crop establishment.	Negative	(Ahmad et al. 2002)
Seedling stage	Reduction in root vigour, root dry weight, shoot dry weight, plant height, leaf expansion, and net photosynthetic rate.	Negative	(Guo-Wei et al. 2011)
Root growth	Reduction in root length and number of secondary roots reduced fresh and dry weight of the roots.	Negative	(Shaheen et al. 2012)
Flowering and Boll development stage	Delayed start of flowering, less fruit-bearing position, fruit shedding, reduced photosynthetic rate, sucrose transformation rate, boll weight and boll size.	Negative	(Peng et al. 2016a)
Fibre quality	Reduced sucrose and cellulose contents, sucrose transformation rate and less activity of metabolic enzymes (alkaline invertase and SPS).	Negative	(Peng et al. 2016b)

4.3 Physiological Mechanisms of Cotton in Response to Salinity Stress

Salinity is secondary stress-causing directly on plant growth by reducing water uptake due to high osmotic potential and absorption of excessive ions creating salt specific ion toxicity (Greenway and Munns 1980; Hafeez et al. 2021). Salinity affects almost all characteristics of plants, including morphological, physiological, and biochemical aspects. It reduces water potential, which causes the closing of stomata, thereby limiting CO_2 fixation (Munns et al. 2006). The most common adverse physiological events are membrane damage, nutrient imbalance, enzymatic inhibition, metabolic dysfunction, photosynthesis inhibition, and hinder other major physiological and biochemical processes leading to retarded growth or death of the plant (Munns and Tester 2008; Alamri et al. 2020). Salinity impaired photosynthesis leads to the destruction of cellular metabolism and ultimately results in abnormal plant growth in cotton (Zhang et al. 2016). The common physiological phenomena in cotton plants are reported as reduction or inhibition of growth and development, reducing major primary metabolic processors such as photosynthesis, respiration, and protein synthesis, etc. (Meloni et al. 2003; Ali et al. 2016). Salinity significantly impacts germination, vegetative growth, and cotton yield with great spatial and temporal variation (Guo et al. 2012). The flowering and boll-forming stages are the key yield-determinant period of upland cotton, which are highly sensitive to salinity (Han and Kang 2001) and thus affect fibre yield directly. The cellular level direct responses to salinity are the imbalance of cellular ions causing ion toxicity, osmotic stress, and reactive oxygen species (ROS) (Khan et al. 2000; Hasanuzzaman et al. 2020). Reports showed that salinity causes the excessive generation of reactive oxygen species (ROS) such as superoxide anion (O^-), hydrogen peroxide (H_2O_2), and the hydroxyl radicals ($OH^\bullet$) in plants (Mittler 2002; Masood et al. 2006), which are harmful or cause deadly damages in cellular environments. Thus, protection against damaging effects from ROS is regulated by the antioxidant enzyme systems of the plants. Superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) are commonly available antioxidants that act against ROS damage (Prochazkova and Wilhelmova 2007; Hasanuzzaman et al. 2020). Proline and glycine betaine are certain osmolytes that accumulate in cellular environments protecting plants from salinity stress (Mitysik et al. 2002; Rontain et al. 2002). The impact of salinity on photosynthesis is a secondary effect that is facilitated by low CO_2 concentrations in the leaves leading to stomatal closure (Meloni et al. 2003; DeRidder and Salvucci 2007).

4.3.1 Growth Responses of Cotton to Salinity Stress

There are two main plant groups (halophyte and glycophyte) based on their level of tolerance to salinity (Cheeseman 2015; Hafeez et al. 2021). Halophytes have a relatively higher tolerance to high salts concentrations (400 mM NaCl), while glycophytes show severely retarded growth under high salinity conditions. Plants evolved certain salt tolerance mechanisms, such as specific salt on the leaf surface for salt secretion. The capacity for secreting salts (by salt glands) is highly correlated with salt tolerance in halophytes (Tester and Davenport 2003; Hafeez et al. 2021). Cotton is reported as a moderately salt-tolerant crop (Ashraf et al. 2010). The varied genotypic differences of response at different growth stages are reported by Ashraf et al. (2008). According to Maas and Hoffman (1977), cotton is classified as the second most salt-tolerant crop, though the degree of tolerance varies among genotypes. The salt threshold level of cotton has been reported as 7.7 dS m^{-1} (Maas and Hoffman 1977; Zhang et al. 2013). Salinity tolerance mechanisms are complex, depending on a wide range of traits controlled by different genetic expressions. Different saline responses were detected in different saline regimes. The variation of growth in cotton genotypes is closely associated with physiological characteristics such as photosynthesis, water use efficiency, and respiration, indicating differential genetic behaviour in biochemical mechanisms (Ziaf et al. 2009).

Cotton responses to salinity are greatly varied with genotypes and growth stages. Seed germination, seedling emergence, and young seedling stage of cotton are more sensitive to salinity (Ahmad et al. 2002), showing delayed germination and seedling emergence (Khorsandi and Anagholi 2009). Reduced plant growth observed in cotton cultivars might be directly associated with a salt-induced reduction in photosynthetic rate and imbalanced water status (Shaheen et al. 2012). Drastic reduction in cotton yield under saline conditions is due to a decline in the number of mature balls as a result of delayed flowering, a high percentage of shedding flowers, and immature balls (Anagholi et al. 2013). Sucrose accumulation in leaf cotton balls is critical for cotton yield, and retarded ball development is noticed under salinity stress due to declined sucrose transportation from leaf cotton balls to developing balls (Peng et al. 2016a). Fibre quality and quantity are economically important parameters of cotton. Quality parameters such as thickness and length of fibre mainly depend on the deposition of cellulose, and hence sucrose metabolism directly involves in cellulose synthesis (Fernandes et al. 2004). Salinity impaired sucrose translocation and thereby cellulose deposition, causing deterioration in fibre quality. A recent report showed that available sucrose is not efficiently converted to cellulose because of altered enzymatic activities under salt stress (Peng et al. 2016b).

4.3.2 Physiological Responses of Cotton to Salinity Stress

Photosynthesis is the key process directly associated with yield. Salinity causes a reduction in chlorophyll contents due to retarded production of enzymes responsible for chlorophyll (Chl) synthesis (Lee et al. 2013), hence directly affecting photosynthesis (Zhang et al. 2014). Further decrease in carotenoids biosynthesis was reported to hinder photosynthetic rate under salt stress (Zhang et al. 2014; Shah et al. 2017). However, carotenoids' degradation rate is lower compared to Chl under salinity stress (Rafique et al. 2003). Cotton genotypes showed a differential response in chlorophyll fluorescence in terms of quantum yield of PSII (Fv/Fm) under high salt concentration (Shaheen et al. 2012). Varietal differences in mitigating oxidative stress by keeping higher antioxidant activities, variations in the Chl a, Chl b, and Chl (a+b) contents, net photosynthetic rate and stomatal conductance, the differential magnitude of activities of SOD, catalase (CAT), APX, and GR were observed in cotton cultivars (Zhang et al. 2014).

Accumulation of salts in different tissues is said to be a salt-resistant mechanism in halophytes. Salt accumulation in tissues varies with genotypes. Certain genotypes showed high concentrations of Na^+ in shoot tissues (Gouia et al. 1994), but in some cases, in roots and leaves (Sun and Liu 2001). Salt secretion through salt glands and leaf glandular trichomes in the leaves to lower salt concentration is another mechanism for salinity tolerance in cotton plants (Peng et al. 2016a). Ion compartmentalization is another strategy for salt tolerance in plants. Species-specific Na^+ and Cl^- compartmentalization is well understood. In particular, high ion concentration was confined to inactive tissues while showing lower ion distributions in active and more sensitive tissues designating ion compartmentalization in tolerant cotton genotypes (Peng et al. 2016a). The higher peak of Na^+ than Cl^- was previously reported in cotton under salt stress (Gouia et al. 1994). Peng et al. (2016c) reported that Na^+ accumulation is significantly high in root vascular cylinder cells of cotton temporarily and transported to shoot later after 48 hours. Thus, cotton shoots have a considerable role in Na^+ compartmentalization capacity for maintaining an optimal cytosolic K^+/Na^+ratio. The high selective absorption of K^+ over Na^+ is regulated by *GhSOS1*, *AKT1* and *HAK-5* genes (downregulation), and *GhHKT1* and *GhNXH1* genes (upregulation) in salt-tolerant cotton genotypes through compartmentalization of Na^+ ion into vacuole facilitating K^+ uptake (Wang et al. 2017).

Also, mesophyll cells contributed to extrude Na^+ and H^+ at high salt environments contributing to Na^+ homoeostasis at the cellular level through Na^+/H^+ transporter and H^+-ATPase in the plasma membrane (Peng et al. 2016b). The net Na^+ efflux of the cotton root at salinity was positively correlated with the net influx of H^+ due to an active Na^+/H^+ antiporter across plasma membrane H^+-ATPase (Kong et al. 2012). The osmotic adjustment by the Na^+ compartment in the vacuole, decreasing Na^+ in the cytosol significantly contributed to salt tolerance in plants (Maathuis 2014). Accumulation of osmoprotectants such as amino acids, sugars, glycine betaine, polyols, and polyamines regulate metabolic processors under salt stress stabilizing the plasma membrane and preventing protein denaturation, maintaining cell turgor facilitating water uptake (Naidoo and Naidoo 2001; Rontain et al. 2002). High expressions of the choline monooxygenase (CAM) gene, which is related to the catalytic pathway for conversion of choline into betaine was detected in cotton transgenics in response to salinity tolerance (Zhang et al. 2009). The choline monooxygenase (CMO) gene (*AhCMO*) overexpressed cotton plants showed enhanced photosynthetic capability (Fv/Fm value) with slighter leaf damages upon exposure to salinity (Zhang et al. 2009).

Under saline environments, many genes have been reported as salinity tolerant viz. 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), tonoplast Na^+/H^+ antiporter (Wu et al. 2004) and 109 WRKY genes (*GarWRKYs*) (Fan et al. 2015). Further, increased expressions of *GhSOS2*, *GhSOS1*, *GhSOS3*, *GhPMA1*, and *GhPMA2* genes have been detected in cotton plants under salinity stress (Peng et al. 2016a). The upregulation of five ABC transporters (Gh_A12G1090, Gh_A10G0583, Gh_A05G1089, and Gh_Sca006272G01), which may have a possible role in salt tolerance, and ABC2 (Gh_A09G1286) in response to Na_2CO_3, NaCl, and NaOH stresses in cotton has been reported (Zhang et al. 2018). Certain aquaporin proteins such as tonoplast intrinsic proteins (TIPs) and plasma membrane intrinsic proteins (PIPs) in cotton were downregulated to conserve water under salt stress (Li et al. 2015). The overexpression of *GhMT3a, GhSOD1,* and *GhCAT1* genes downregulated the ROS and reported high tolerance to salt in transgenic cotton (Lu et al. 2013). Cheng et al. (2018) reported that co-expression of *AtNHX1-TsVP* genes showed greater seed yields in cotton under salinity, contributing Na, K, and Ca ion accumulations in salt-affected cotton leaves adjusting osmotic potential to maintain turgor and carbon fixation.

4.3.3 Salinity Tolerance Mechanism in Cotton

Salinity adversely affects the seed germination process (rate and delay of germination), leading to sub-optimal crop establishment and finally reduces crop yield. It has been claimed that salt stress delays and reduces the germination percentage (GP) in cotton due to osmotic stress and Na+ and Cl's negative effect (Sattar et al. 2010). Seed priming is a pre-sowing treatment used to advance germination through controlled hydration but to a level not sufficient for complete germination. It is used to increase the germination rate and reduce the time required for germination and emergence by alleviating the adverse impacts of saline stress. Several priming techniques, viz., hydro-priming, osmo-priming, halo-priming, matric priming, thermo-priming, priming with plant growth hormones, bio-priming, and drum priming are used. Priming contributes to metabolic repair in seeds and increases the germination rate, induces osmotic adjustment, and reduces germination time under salt stress (Ashraf and Foolad 2005; Bilqees et al. 2019). Seed priming practice overcomes the adverse effects of salinity stress during germination (Bradford 1986). Hydro-primed cottonseeds increased germination and emergence percentage, plumule and radicle lengths, dry seedling weight, and reduced the total germination period, as well as enhanced stand establishment, showing superior plant height, dry weight, and leaf area (Ahmad et al. 2012). Priming of cottonseed with H_2O_2 improved germination by enhancing the concentration of abscisic acid (ABA), and gibberellic acid (GA) through down-regulation of *NCED5* and *NCED9*, and *GA2ox1* genes, respectively (Kong et al. 2017). In addition, priming with potassium nitrate also remained effective in increasing the germination, emergence vigour, length of plumule and radicle, dry weight of seedling and plant, plant length, and leaf area plant^{-1} (Bozcuk 1981). Moreover, priming with kinetin boosted germination rate (Bozcuk 1981), seed priming with calcium led to higher shoot length (Kent and Läuchli 1985).

Higher concentrations of salts in soil solution inhibit cotton growth, reproductive development, and lint yield, especially in arid and semi-arid regions of the world. Irrigation water having higher salt concentrations results in their accumulation of Na^+ and Cl^- ions leading to the severe decline in the yield of seed cotton. Boosting cotton tolerance to salt stress can impart yield stability and limit the salinization process through drastic reductions in inputs. To date, targeted breeding for improving salinity tolerance in cotton has remained limited in scope, especially regarding attaining reliable botanical traits and physiological mechanisms against salinity. Among salinity tolerance mechanisms of cotton, reduced accumulation of salt ions and organic solutes synthesis are the leading mechanisms that help the stressed plants in offsetting the effects of salinity (Naidoo and Naidoo 2001). For instance, limited uptake of Na^+ from soil solution is one of the most pertinent traits which imparts salinity tolerance to cotton plants.

4.3.3.1 Production of Organic Solutes

To cope with the adverse effects of salinity, cotton plants accumulate numerous osmoprotectants like glycine betaine, polyamines, amino acids, sugars, proline, and polyols. These osmoprotectants assist plants in metabolic adjustment and ultimately impart salt tolerance. Inside the vacuole, balancing the osmotic potential is done through the compartmentalization of organic ions. Besides, organic solutes offer a shield against protein degradation by imparting stability to membranes and maintaining cell turgor and the output of gradient force, which triggers uptake of water (Rontain et al. 2002). Certain inorganic ions like K^+ and Na^+ and organic osmolytes like proline play key roles in salt tolerance. Plants can protect themselves from salt toxicity by maintaining higher K^+ content and K^+/Na^+ ratio and/or organic solutes.

4.3.3.1.1 Proline

Among organic solutes, proline assists in RUBISCO stabilization and its functionality maintenance under severe salt stress (Ahmad et al. 2002). The concentration of proline in Egyptian cotton, as well as tree cotton, gets multiplied (36 and 121% in roots and leaves, respectively) in the presence of NaCl (Meloni et al. 2001). Contrarily, no significant alterations in proline content under salt stress have also been reported in cotton (Ullah et al. 2016; Golan-Goldhirsh et al. 1990). Although proline performs a vital role in offsetting salinity effects if it remains contained in the cytosol, it cannot adjust osmotic pressure on its own.

4.3.3.1.2 Glycine Betaine

Glycine betaine is an osmoprotectant that plays an essential function and fast accumulates in various plants throughout environment stress (EL Sabagh et al. 2019a, 2019b; Ali et al. 2020). In response to heat and salt stresses, glycine betaine is another prime osmoprotectant synthesized by cotton plants (Quan et al. 2004). Osmotic adjustment is the major role of glycine betaine under salinity stress (Khan et al. 1998b). In transgenic cotton, the CAM gene has been reported to be responsible for more elevated glycine betaine production, which imparts salinity tolerance (Zhang et al. 2009).

4.3.3.2 Membrane and Transport

Cotton plants tend to regulate the flux of ions, which leads to considerably lower retention of salt ions. Contrary to salt-stressed conditions, a high K:Na ratio is usually maintained in the cytosol of plant cells having lower Na concentration and higher K level (Higinbotham 1973). However, disturbance in K:Na ratio, especially in favour of sodium ions that get accumulated in plants roots causing hyperosmotic stress and ion toxicity. Under the saline condition, the ionic imbalance gets disrupted as hydrated forms of Na and K become similar, rendering K influx pathway unable to differentiate between Na and K ions. Thus, Na ion influx passes through the K influx pathway leading to Na toxicity in the cell cytoplasm. To maintain K:Na ratio, cotton plants reduce Na influx in roots, compartmentalize Na in cell cytosol to vacuole, and make Na efflux from root cells. The primary active transport facility is utilized by plant cells to trigger a salt over-sensitive (SOS) pathway to initiate Na efflux, leading to a high K:Na ratio in the cytosol (Zhao et al. 2013). Along with K:Na ratio, the maintenance of a higher ratio of Ca:Na is of utmost importance, enabling plants to cope with salt stress. Salt tolerant genotypes of cotton have higher K absorption compared to Na, which is maintained and downregulated by *GhSOS1, HAK-5,* and *AKT1* along with *GhHKT1* and *GhNXH1* upregulation. Thus, it becomes evident that cotton genotypes salt tolerance may be regarded as directly linked with K:Na compartmentalization and higher uptake of K (Wang et al. 2017).

4.3.3.3 Antioxidants

Salt tolerant genotypes of cotton exhibit higher antioxidants activity, which is directly associated with salt tolerance levels (Noreen and Ashraf 2009). Salinity causes the initiation of ROS, including hydrogen peroxide, hydroxyl radical, and superoxide synthesis (Monsur et al. 2020). The accumulation of ROS under saline conditions causes oxidative stress, nucleic acid mutation, protein denaturation, and destruction, along with severely disturbing the metabolism process (Yassin et al. 2019). Contrary to salt stress conditions, these ROS get neutralized by intercellular antioxidants under normal conditions (Czegeny et al. 2014). To alleviate the drastic effects of salinity-induced oxidative stress, cotton plants utilize enzymatic and non-enzymatic antioxidant systems. The enzymatic system of antioxidants carries CAT, peroxidases (POD), SOD, and glutathione peroxidase, and numerous enzymes of APX, ascorbate–glutathione peroxidase, and GR. Among antioxidant enzymes, SOD is considered vital as it regulates the concentration of O_2^- and H_2O_2. Also, the scavenging ability for ROS has been demonstrated by APX and CAT. However, their scavenging ability multiplies in the presence of SOD (Zhang et al. 2016). While among non-enzymatic antioxidants, carotenoids ascorbic acid, glutathione, and tocopherols are most prominent (Ashraf et al. 2008; Foyer and Noctor 2000). Under saline conditions, cotton exhibits intensified activity of SOD and POD activity, which leads to a higher photosynthetic rate and ultimately enables plants to offset the drastic effects of salinity (Zhang et al. 2014). Ascorbic acid is a vital non-enzymatic antioxidant that tends to multiply its concentration in chloroplast and cytosol under saline conditions. It also plays a role in protecting photosynthetic machinery. Furthermore, it has been revealed that enzymatic antioxidant activity increased during salt stress at the fibre development stage of cotton (Rajguru et al. 1999). Thus, both enzymatic and non-enzymatic antioxidants systems tend to impart tolerance in cotton plants against a saline environment.

4.3.4 Improving the Root Zone Environment

Cotton plants are susceptible to salt stress at the emergence and young seedling stages than any other growth stage. Good stand establishment is a prerequisite for higher yield of cotton, and thus proper field management should be taken for good emergence and stand establishment under saline conditions (Dong et al. 2008). Poor stand establishment and seedling growth are often encountered in saline soils. Salinity stress is originated from the root zone soil environment. Unequal salt distribution in the root zone alleviates salt damage to cotton plants (Dong et al. 2010a). Therefore, any practice that improves at the least part of the root zone environment can alleviate salt damage. Ways to improve root zone environment include reduction of soil salinity by increasing soil moisture and temperature. The entire root system of cotton plants exposed to NaCl significantly reduced the shoot dry weight, leaf area, plant biomass, leaf chlorophyll, photosynthesis, and transpiration, economic and biological yields compared to the NaCl-free control. In contrast, the inhibition effect of salinity on growth and yield was significantly reduced when only half of the root system was exposed to low-salinity (Dong 2012a). Dong et al. (2008) found that furrow-bed seeding induced unequal salt distribution in saline fields and significantly improved the plant growth, yield, and earliness than flat beds seeding in cotton. The improvement of yield and earliness was mainly due to the unequal distribution of salts in the root zone (Dong 2012a). Unequal salt distribution increased water use efficiency, K^+ and K^+/Na^+ ratio, and decreased Na^+ accumulation in leaves (Kong et al. 2012). Recirculation of Na^+ from the shoot to the low-salinity side of roots through the phloem is an important mechanism for reducing 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 (Dong 2012a).

4.4 Agronomic Management

4.4.1 Mulching and Furrow Seeding

Mulching can alleviate salt damage of cotton plants in saline fields. Plastic mulching (covering row with polyethylene film) is common in many countries to conserve soil moisture. It enhanced plant growth and cotton lint yield by increasing soil temperature, water conservation (Dong et al. 2007), controlling weeds, and saline toxicity in the root zone (Dong 2012b). Plastic mulching developed the root system of cotton plants in relatively low-saline soil, reducing the damage to plant growth under salt conditions (Bezborodov et al. 2010; Dong et al. 2010a). It is also reported that the integration of plastic mulching with furrow seeding more effectively enhanced the stand establishment, earliness, yield components, and yield of cotton than mulching or furrow seeding alone (Dong 2012b). A combination of plastic mulching with furrow seeding augmented the unequal salt distribution. It elevated soil temperature and moisture in the root zone soon after seeding, resulting in reduced uptake of Na^+ in roots and leaves, peroxidation of lipids in cotton tissues, and increased Pn. It has been argued that the integration of plastic mulching with furrow bed seeding is a promising cotton production technique in saline areas (Dong et al. 2008; Dong et al. 2010). Generally, plastic mulching is used after sowing, but pre-sowing evaporation in spring enhances the accumulation of salts and moisture loss from the surface layer of saline-affected soils. Early mulching is also a promising cotton production technique in the saline areas, which reduces moisture loss, elevates soil temperature, and controls root zone soil salinity (Dong et al. 2009). Hence, 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 (Dong 2012b).

4.4.2 Late Planting of Short-Season Cotton

Late planting of short-season cotton is a promising system for growing cotton in saline-affected areas. Normal planting of full-season cotton in saline fields in temperate areas is faced with poor stand establishment, late maturity, and increased inputs cost. 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 in a saline field. The yield from late-planted short-season cotton performed better in earliness and required less input than normal-planted full-season cotton. Therefore, the net returns from late-planting of short-season cotton are greater than those from normal-planting of full-season cotton.

4.4.3 Plant Density Management

Many earlier studies (Francois 1982; Feinerman 1983) have indicated that increased plant density under salinity stress considerably increased the cotton yield. Usually, growth and plant size is reduced in excessive saline soils (Khan et al. 2004), and the smaller plant size left a significant space between plant canopies, which could support additional plants to grow (Francois 1982). It has been reported that increasing plant population enhanced the earliness of cotton (Fowler and Ray 1977). Dong (2012a) concluded that the seed cotton yield is greatly improved by increasing plant density under strong salinity conditions. It is suggested that increased plant density would be necessary for enhancing the yield and earliness of cotton in highly saline fields.

4.4.4 Fertilizer Management

Plant growth, nutrient absorption and metabolism, protein synthesis, and water absorption are greatly altered under salt stress and ultimately reduced the uptake and full utilization of plant nutrients (Ella and Shalaby 1993; Pessarakli 2001). Proper fertilizer management in saline-affected soil increased the yield of cotton (Xin et al. 2010). Application of over-dose fertilizers as in soil, foliar, or both successfully alleviated the salt stress effects and increased cotton yield. Inhibition of cotton growth due to salinity is alleviated by the application of nitrogenous fertilizer (Chen et al. 2009). At the beginning of an irrigation cycle, the application of N enhanced yield and fertilizer use efficiency (Hou et al. 2009). Both soil and foliar application of N in cotton plants under saline condition (12.5 dS m^{-1}) improved plant growth and salinity tolerance by increasing uptake and balanced distribution of N across tissues, K^+ and ratio of K^+ /Na^+ (Dong 2012b). These findings may be of significance for nitrogen management for cotton in highly saline soils. The uptake of K is decreased in saline soil. Keshavarz et al. (2004) indicated that the application of K in soil improved the growth and yield of cotton under saline conditions. Foliar application of KCl (@500 mg/L) and NH_4NO_3 (@500 mg/L) alone or in mixture alleviated the detrimental effects of salt stress by improving vegetative and reproductive parameters in cotton (Jabeen and Ahmad 2009). Cotton plants treated with NPK fertilizer as soil application under saline conditions significantly increased nutrient uptake, decreased Na^+ uptake, and produced the highest biomass and lint yield (Xin et al. 2010).

4.4.5 Increasing Soil Moisture and Temperature

It has been declared that seed emergence and seedling growth is improved due to increasing soil moisture and temperature under salinity stress condition (Dong 2012b). Cottonseeds were sown in pots containing different levels of saline soils collected from saline fields in the Yellow River Delta with different moisture content (12, 16, and 18%) by Dong (2012c), and reported that the emergence and seedling growth is increased with increasing soil moisture levels. The higher level of moisture diluted the saline toxicity effect and decreased the osmotic stress and Na^+ accumulation in leaves, resulting in improved seedlings' emergence and growth (Dong 2012c). In another study, Dong (2012c) sown cottonseeds in potted saline soils at varying dates to determine soil temperature effects and depicted that soil temperature ranging from 20 to 30°C is beneficial for seedling emergence and growth under salinity stress.

4.4.6 Water Management Strategies

Plant growth of cotton is reduced due to low-quality irrigation water with high EC, sodium adsorption ratio (SAR), residual sodium carbonate (RSC), and pH value, which are the reasons for salinity stress (Murtaza et al. 2006). Therefore, a judicious water management strategy is crucial for successful cotton cultivation against salinity stress. The use of good quality water is crucial for better soil management, plant growth, and productivity under a saline environment because it drains out or leaches down soluble salts from the root zone (Ezeaku et al. 2015). Surface water should be used instead of salty sub-surface water for irrigation in crop fields. In salty sub-surface water, it is advised to use gypsum, which increased grain yield in rice and wheat under salinity (Zaka et al. 2009). In addition to this, the use of gypsum with surface irrigation water helps to reduce ECe, pH value, and SAR of soil at 0–30 cm depths (Mehdi et al. 2013).

4.5 Application of Growth Hormones

Hormonal imbalance is one of the important impacts that salinity has on plants. There are many plant growth regulators (PGRs) being used to induce plant growth and bolls development in cottons, such as aminoethoxy vinyl glycine (AVG), ethephon, and 1-methyl cyclopropane (1-MCP) for ethylene inhibitor under salt stress (Hussain et al. 2019b). Likewise, exogenous applications of ABA, brassinosteroids (BRs), or their analogs (D-31, D-100, etc.) are good options to improve plant performance under salinity stress (Singh et al. 1987; Ashraf et al. 2010).

4.6 Conclusion

Among abiotic stresses, soil salinity has emerged as one of the most serious threats that significantly reduce the yield and quality traits of cotton by altering the physiological and biochemical processes at different growth stages. Cotton plants tend to cope with soil salinity, generally activate different physiological and biochemical mechanisms by changing their morphology, anatomy, water relations, photosynthesis, protein synthesis, primary and secondary metabolism, and biochemical adaptations such as the antioxidative metabolism response. Globally, there is a dire need to increase our understanding of soil salinity's adverse impacts on cotton growth and lint yield along with fibre quality, particularly in arid and semi-arid regions, in order to ensure sustainable production of the fibre under changing climate. The underlying mechanisms of salinity tolerance like biosynthesis of antioxidants and other chemical compounds Different agronomic management practices such as late planting of short-season varieties, seed priming with growth regulators, using mulches, planting density management as per pedo-climatic conditions, and fertilization management have the potential to boost the cotton ability to cope with drastic effects of the saline environment. Therefore, breeders and producers need to understand the influence of salinity on crops for improvement in production, protein, and oil quality (amino and fatty acid) under saline conditions. Modern biotechnological tools such as omics approaches include genomics transcriptomics, metabolomics, proteomics, genome editing tools like CRISPR/Cas system, and speed breeding on a large scale can boost our knowledge and help scientists in developing salt tolerance ready-to-grow cotton genotypes or lines.

Conflicts of Interest

The authors declare that they have no conflicts of interest to report regarding the present study.

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