

UNDERSTANDING AND MITIGATING THE IMPACTS OF DROUGHT STRESS IN COTTON- A REVIEW

Muhammad Farrukh Saleem¹, Muhammad Aown Sammar Raza^{2,*}, Salman Ahmad², Imran Haider Khan¹ and Abdul Manan Shahid²

¹Department of Agronomy, University of Agriculture Faisalabad, Pakistan; ²Department of Agronomy, University College of Agriculture & Environmental Sciences, The Islamia University of Bahawalpur, Pakistan.

*Corresponding author's e-mail: aown_samar@yahoo.com, aown.sammar@iub.edu.pk

Water scarcity is the most serious abiotic stress restricting plant productivity throughout the world. Losses in crop yield due to drought exceed from losses caused by other environmental factors. In this review article different morphological, physiological and yield attributes of cotton under drought stress, mechanism of drought induced losses and various management strategies to mitigate drought stress have been discussed. Drought stress reduces growth of leaf, stem and root, interferes with leaf water relations, photosynthesis, respiration, reduces water-use efficiency and ultimately yield of cotton. Under water deficit conditions cotton shows various responses to cope with drought stress. The major mechanisms include accumulation of osmoregulators, plant growth regulators and production of heat shock proteins. Different management strategies to alleviate water deficit stress like foliar application of osmolytes, potassium and growth regulators (hormones), various drought responsive genes, proteins at molecular level, screening and breeding programs against drought tolerance and mulching are also discussed in this paper.

Keywords: Abiotic stress, irrigation water, crop productivity, water deficit, production strategies

INTRODUCTION

Cotton (*Gossypium hirsutum* L.) is one of the most important global cash crops. It is considered as world's leading oil and fiber producing crop (Fryxell, 1992) and is most important crop for smallholders in many of the Asian and Latin American countries (Fortucci, 2002).

Crop productivity in many regions of the world is adversely affected due to shortage of irrigation water (Sinclair, 2005). Drought is a world-spread abiotic stress (Hongbo *et al.*, 2005). Decline in crop growth and productivity were reported when suffered from water deficit stress (Farooq *et al.*, 2008). Yield losses in crops due to drought are perhaps more than the losses due to other abiotic causes (Table 1). Decline in potential yield of various crops due to drought ranges between 54% and 82% (Bray *et al.*, 2000). Every phase of plant growth and development was affected by drought because water is essential for every stage of plant from seed germination up to plant maturity (Chaves and Oliveira, 2004). Water deficit stress also affects the plants by modifying the morphology, anatomy, physiology and ultimately the yield of the crop (Raza *et al.*, 2012a). Various plant processes like expansion of leaves, organ development (both leaves and fruit), growth and function of roots, photosynthesis, boll production and retention and length and thickening of fiber are badly affected under drought stress. Therefore, for sustainable crop production, it is prerequisite to alleviate the damaging effects

of drought by various management practices (Mahajan and Tuteja, 2005).

The deficit water conditions due to high temperature and less rainfall during the last few years poses a serious risk to the cotton productivity. It is, therefore, very important to explore strategies to cope with this hazardous problem. The economic and efficient use of water is one of the best ways to tackle this problem (Nasrullah *et al.*, 2011). Many strategies like spray of some nutrients (Raza *et al.*, 2012b, 2015) and compatible solutes (Raza *et al.*, 2012c, 2015), bed sowing and use of mulches (Ahmad *et al.*, 2015) have been developed to overcome deficit water conditions (Schahbazian and Nejad, 2006).

Table 1. Cause of crop loss proportion of payment (%).

Abiotic stress	Estimate of loss %
Drought	40.8
Excessive water	16.4
Cool	13.8
Hail	11.3
Wind	7.0
Flood	2.1
Others	1.5

Source: Boyer (1982)

Effect of Drought Stress on Various Morphological Characteristics of Cotton: Drought stress adversely affects the plant growth, development and yield throughout the world

(Boyer, 1982). Water-deficit stress impaired various morphological traits like reduction in cell and leaf expansion, stem elongation, root shoot ratio, number of nodes and leaf area index of cotton (Gerik *et al.*, 1996). Reduction in cell expansion caused by drought affected the leaf, stem and root growth of cotton to a significant level (Hearn, 1994). Pettigrew (2004) observed that water-deficit stress caused reduction in leaf size of cotton. Pace *et al.* (1999) also observed fewer number of nodes, reduced plant height, leaf area, less leaves on both main and sympodial branches, lower fresh and dry weights of leaves, stem and root in cotton plants grown under water deficit conditions compared to plants under control conditions.

Germination: Evaluation of seeds' germination capacity is one of the commonly used indicators of plants' tolerance to water deficit stress (Larcher, 2000). Henrique *et al.* (2011) tested four cotton varieties in germination chamber at different osmotic potentials to determine the effects of drought on cotton germination; germination percentage decreased with increase in osmotic potential and completely inhibited at -1.0 MPa. Similarly, Pereira *et al.* (1998) tested ten cotton genotypes and found that germination percentage was completely restricted at -1.0 MPa. Inhibition of germination capacity of seeds is due to limited accessibility of water for seed imbibitions (Rauf *et al.*, 2007).

Germination velocity index (GVI), a ratio of average number of seeds germinated per day (Nakagawa, 1994), is a more sensitive indicator to measure the effects of osmotic stress than the germination potential (Dias and Marcos Filho, 1996). GVI value for cotton cultivars was also reduced with decreased values of osmotic potential (Henrique *et al.*, 2011).

Shoot growth: Stem growth and plant height are often decreased under drought. Reduction in stem diameter under drought was observed due to imbalance in water relations (Simonneau *et al.*, 1993). It is well known that an increased concentration of ABA in plants under drought conditions has an inhibitory effect on shoot growth (Achar *et al.*, 2006). Plant height was sensitive to water supply; high water levels significantly raised the height. The highest mean plant height was measured in the full irrigation treatment and the mean plant height was reduced with decreasing levels of irrigation (Yagmur *et al.*, 2014).

Hussein *et al.* (2011) planted cotton at different irrigation regimes and concluded that maximum plant height was observed in full irrigation treatment and plant height decreased as the amount of water application decreased. Ihsanullah (2009) screened 32 cotton varieties for drought tolerance under different irrigation levels and observed that reduction in plant height across water regimes ranged from 13 to 47%.

Root growth: Drought not only decreases the stem growth and plant height but also the root growth. However, root growth is less affected by drought than that of shoot (Quisenberry and McMichael, 1991). Under drought condition, water uptake by

plants from the soil primarily depends upon the extension of roots (Richard and Passioura, 1981).

Root elongation during water deficit conditions may help plants to get water from deeper soil layers, thus avoiding drought (Ludlow and Muchow, 1990). However, longer roots may reduce shoot growth by the partitioning of more photosynthates towards roots at the expense of shoot. So, increase in root shoot ratio of plants is also a common effect of drought, caused by more investment of assimilates in roots. Quisenberry and McMichael (1991) observed an increased root:shoot ratio under terminal drought condition. Pace *et al.* (1999) measured the root and shoot parameters of cotton grown under drought and observed reduction in growth, development, and distribution of stressed cotton plants roots as compared to control treatments. Similarly, reduction in root dry matter due to water deficit in cotton plant has been observed by Ferreira *et al.* (2013).

Table 2. Effect of drought on different vegetative parts of cotton.

Plant part	Drought	Control
Stem height (cm)	20.0±(1.10)*	27.9±(1.40)
Stem dry weight (g/plant)	1.13±(0.05)*	1.39±(0.06)
Leaf dry weight (g/plant)	1.41±(0.10)*	2.16±(0.33)
Node number	7.80±(0.30)*	9.40±(0.50)

*Means in a row are significantly different at the 0.05 probability level; Source: Pace *et al.* (1999).

Leaf area: Leaf area is one of the main determinants of crop yield as it regulates plant water balance through its influence on transpiration (Levitt, 1980). Leaf expansion is the most sensitive growth process affected by drought (Alves and Setter, 2004). Leaf senescence and abscission were accelerated when cotton plants were grown under water deficit conditions. Under well water supply leaf area index increases along with growth rate, but it decreases in water deficit condition due to leaf area adjustment process.

Several studies have shown that drought stress results in poor cotton canopy development. Ihsanullah (2009) concluded that the number of leaves on sympodial branches of cotton decreased when exposed to drought. Parida *et al.* (2007) conducted a pot experiment in green house on two cotton varieties and observed 24% and 29% decrease in leaf area of two genotypes respectively, in drought-stressed plants as compared to the control treatments. Rosenthal *et al.* (1987) planted cotton in green house and determined that leaf growth was severely inhibited when the percentage of soil-available water was less than $51 \pm 15\%$. Kies (1982), found that leaf area of upland cotton in dry treatment of 1.50 MPa soil moisture potential was 33 percent less than in a wet treatment of - 0.5 MPa soil water potential.

Noreen *et al.* (2013) conducted experiments on cotton grown under drought conditions to study the effects of water deficit stress on leaf area at various reproductive growth stages in

cotton and concluded that drought decreased leaf area in all stages except maturity (Table 3)

Table 3. Leaf area index of cotton at different growth stages under control and drought conditions.

Name of stage	Control	Drought	LSD (p<0.05)
First flower bud	0.32	0.29	0.01**
First flower	1.22	0.95	0.06**
Peak flowering	3.11	2.60	0.06**
First boll split	2.40	2.00	0.09**
Maturity	0.68	0.68	0.08**

Water Related Parameters:

Excised leaf water loss (ELWL): Excised leaf water loss and leaf water potential are the common measures of leaf water stress (Jones *et al.*, 1991). ELWL indicates the thickness of cuticle because after excision from plant, water loss of leaves occurs through epidermis. Haque *et al.* (1992) reported that transpiration is affected by both waxiness and cuticular thickness of leaf surface. So, lower rate of transpiration and excised leaf water loss are important criteria for selection of crop plants against drought stress (Rahman *et al.*, 2000).

ELWL showed negative correlation with agronomic traits as well as the stomatal size, stomatal frequency and relative water content. However, the absence of the correlation of ELWL with all the other studied traits shows that the genes for ELWL segregate independent of the other traits so plants with lower ELWL (having drought resistance) may be selected for good quality and yield traits (Malik *et al.*, 2006). It has been observed that the species having low rate of water loss through leaf cuticle are better adapted to dry environment. Excised leaf water loss, measured directly on leaf fresh, wilted and dry weight basis, was adversely affected by limited water supply in all the cotton genotypes under study (Soomro *et al.*, 2011) (Table 4).

Table 4. Excised leaf water loss in some cotton varieties under control (7 irrigations) and drought (2 irrigations) conditions.

Varieties	Control	Drought stress
CRIS-134	0.86	0.17
CRIS-54	0.71	0.46
CRIS-79	0.97	0.62
CRIS-82	1.18	1.13
CRIS-83	1.19	0.37
CRIS-85	0.61	0.10

LSD for treatments (0.05) = 0.001; LSD for varieties (0.05) = 0.240

Relative water content (RWC): The leaf relative water content (RWC) is a measure of leaf water status and is a good indicator of drought tolerance in plants (Sanchez-Blanco *et al.*, 2002). It is closely related with plant water potential (Ober *et al.*, 2005).

Many leaf physiological traits such as stomatal conductance, leaf turgor, transpiration, photosynthesis and respiration influenced the leaf relative water content (Kramer and Boyer, 1995). Leaves RWC have a significant effect on photosynthesis; Patil *et al.* (2011) observed 50 percent reduction in net photosynthesis when RWC were less than 80 per cent.

Leaf RWC was significantly decreased by drought stress (Faizan ullah *et al.*, 2012). Parida *et al.* (2007) conducted a pot experiment in green house on two cotton varieties and observed that RWC of cotton leaves were 75% and 68.4% in two genotypes, under control conditions while the drought stress caused a decrease in RWC to 72% and 63.7%, respectively.

Yield Parameters: Cotton yield is determined by a combination of factors. Some important parameters are boll number and size, seed number per boll and lint percentage. Environmental conditions significantly influence the physiological activity of the cotton and yield contributing parameters.

Bolls: One of the important yield parameter used as a selection criterion to determine drought tolerance is number of bolls. A strong relationship exists between the cotton yield and number of bolls and under water-deficit conditions boll retention is an important determinant of yield in cotton (Rahman *et al.*, 2008). Timing and intensity of drought mainly affects the cotton yield (Ihsanullah, 2009). In cotton both boll production and retention can be decreased by drought stress. Reduction in number of bolls and weight at the early square stage is the main cause of low seed cotton yield (Unlu *et al.*, 2011; Sarwar *et al.*, 2012). Pettigrew (2005) indicated that 19% reduction in the number of bolls reduced the lint yield of cotton by 25%. Reduction in number of bolls under drought may be due to hormonal imbalance in squares and bolls that could contribute to shedding (Basal *et al.*, 2009).

Drought stress at peak flowering and fruit-setting stages caused fewer number of fruiting positions, shedding and poor development of bolls (Aujla *et al.*, 2005). Basal *et al.* (2009) reported decreasing boll weight with decreased water application. Drought stress reduced the number of bolls and boll weight mainly due to decreased leaf area expansion and photosynthetic production. Hussein *et al.* (2011) observed an increase in number of bolls per plant by increasing the amount of irrigation water; the control plants showed maximum number of bolls.

Seed and biological yield: In most crop plants, most sensitive stage to drought stress is reproductive development (Selote and Khana-Chopra, 2004). According to Reddell *et al.* (1987) most sensitive stage to water deficit stress in cotton is early flowering, while Orgaz *et al.* (1992) observed most damaging effects of drought on cotton yield when applied at peak flowering. In view of Cock and Elzik (1993) boll

development phase of cotton is most sensitive to drought stress.

Yield of the cotton plant is determined by a combination of factors like boll number, weight and size, seed number per boll, and fiber per seed. These parameters are influenced by many physiological processes and their interaction with the environment. Many studies revealed that drought affects yield by disturbing leaf photosynthesis and plant water relations, nutrient relation, dry matter partitioning, biological yield, seed yield as well as lint yield in cotton. Ihsanullah (2009) tested 32 cotton varieties under different irrigation levels and concluded that water stress caused mean reduction of 42% in seed cotton yield and 55% in biological yield across the genotypes.

Under water stress lint yield is generally reduced because of fewer flowers and bolls production (Gerik *et al.*, 1996) and increased loss of fruiting positions (Pettigrew, 2004).

Fiber extension is also sensitive to high temperature and drought stress (Mert, 2005). Both fiber length and strength, affected badly when drought stress was applied at early and 50 percent boll opening stage (Yagmur *et al.*, 2014). Maximum fiber length, strength and fitness were recorded under full irrigated treatment as compared to drought stressed treatments. Reduction in fiber length was due to loss of turgor which disturbed the physiology of cell expansion and resulted in poor yield and quality of fiber (Basal *et al.*, 2009).

Water use efficiency (WUE): Water use efficiency is an important trait to estimate drought tolerance of crops. Many physiological traits like stomatal conductance, photosynthesis, osmotic regulation and root characteristics are associated with WUE (Bacon, 2004). WUE also depends on many morphological characteristics of plants like shape and size of leaf, canopy structure and management practices like row to row, plant to plant distance, planting density and proper plant protection measures (Krieg, 2000).

Availability of water and water use efficiency directly affects the plant growth (Basal *et al.*, 2009) and with increase in WUE growth can also be increased. It is reported that photosynthesis mainly influenced the WUE (Radin, 1992). Genes responsible for regulation of stomata also regulate water use efficiency (Chaves and Oliveira, 2004). Thus WUE mainly concern with gaseous exchange process through stomata.

Indeterminate growth habit is positively correlated with water use efficiency. WUE can vary with leaf age, node and fruiting positions in cotton (Quisenberry and McMichael, 1991). WUE also depends on leaf morphology, thickness and position in the canopy. Loveys *et al.* (2003) reported that change in the CO₂ and H₂O fluxes in and out of the leaf was due to changes in leaf size and affected by leaf thickness due to its effect on rate of evaporation from leaf surface. Moreover, higher values of WUE were reported in leaves under shade than leaves directly exposed to the sun (Sellin *et al.*, 2011).

Blum (2005) reported that maximum use of soil moisture is vital component of increasing WUE. On the basis of various experiments on water use efficiency of cotton, reports have shown that water use efficiency of cotton ranges between 0.1 to 0.3 kg lint m⁻³ of water used (Hearn, 1994).

Harvest index: Harvest Index reflects the partitioning efficiency of photosynthates towards economic parts (Okogbenin *et al.*, 2003). Increase in harvest index is the indicator of crop improvement. Wild ancestors of crops showed poor harvest index because of survival mechanisms, contrary to maximizing the yield (Richards *et al.*, 1998). In general, yield can be enhanced by increasing harvest index.

Environmental changes have significant effects on HI. Drought stress significantly reduced the HI. The harvest index decreased as the level of irrigation water applied was decreased (Hussein *et al.*, 2011) due to drastic effect of water stress on grain weight (Sara and Fatahi, 2013). This suggests that poor growth during drought stress resulted in poor assimilate partitioning towards economic parts.

All the 32 genotypes tested by Ihsanullah (2009) exhibited better HI in well watered as compared to limited watered treatment. Hussein *et al.* (2011) reported more HI in cotton under mild drought stress. However, under severe drought, value of HI decreased as compared to mild drought. Drought applied at different growth stages of cotton decreased HI and highest reduction was observed when drought was imposed at flowering stage (Silva *et al.*, 2010).

Physiological Parameters: The water deficit stress adversely affects a number of physiological processes in plants; disturbs stomatal conductance, rate of transpiration, pigment content of leaves, rate of photosynthesis, ATP content (Lawlor and Cornic, 2002), causes inhibition of enzymatic activities (Ashraf *et al.*, 1995); ionic imbalance and disturbances in solute accumulation (Khan *et al.*, 1999).

Photosynthesis: Photosynthesis is the key process to determine the growth and yield of crops and is directly influenced by water contents of leaf. With decreased water potential and relative water content of leaves photosynthetic rate in leaves also declined (Lawlor and Cornic, 2002). Under water deficit conditions, disturbance in both stomatal and non stomatal factors causes a reduction in photosynthesis of cotton (Leidi *et al.*, 1999).

Under drought stress conditions the main reason for decreased photosynthetic rates is the less diffusion of CO₂ from atmosphere to the carboxylation site in leaves (Chaves and Oliveira, 2004). Reduced CO₂ diffusion is due to combined effect of stomatal closure and reduction in conductance of mesophyll cells (Warren *et al.*, 2004).

Stomatal factors: Although decreased stomatal conductance would result in minimum water loss and allow the plants to survive under severe drought (Sadok *et al.*, 2012), stomatal closure decreases the inward flow of CO₂ into the leaves. As a result of lower CO₂ concentration into the leaf, rate of photosynthesis decreased (Flexas *et al.*, 2004). Boyer (1970)

observed resistance in stomatal conductance of cotton, and found that water potential in the range of -0.8 to -1.2 MPa had drastic effect on stomatal conductance. Bielora *et al.* (1984) planted cotton in pots under normal and water deficit conditions and reported that reduction in stomatal conductance was considerably higher in water-deficit stressed plants than control. Silva *et al.* (2012) observed higher temperatures in water-limited cotton plants than well-watered crop and stomatal conductance to water vapors markedly decreased under limited water supply. Soomro *et al.* (2011) evaluated 31 cotton genotypes under control and water deficit environments; although intervarietal differences were quite evident however, all varieties showed decrease in stomatal conductance under deficit water conditions compared to control.

Non-stomatal factors: According to Silva *et al.* (2012), there was decrease in activation state of Rubisco under water limited conditions. Enahli and Earl (2005) reported that under water-deficit conditions velocity of carboxylation of Rubisco, capacity of regeneration of ribulose-1,5-bisphosphate (RuBP), CO₂ concentration at the site of carboxylation and activity of ATP-synthase decreases, resulting in a decline in photosynthetic activity (Tezara *et al.*, 1999). Massacci *et al.* (2008) observed that under water deficit stress transport of electrons produced during light reaction is increased due to over excitement of reaction centers of photosystem II. As a result over-production of damaging reactive oxygen species was also observed.

Under drought stress 2-carboxyarabinitol- phosphate is formed in many plants during night which binds strongly with Rubisco and restricts its catalytic activity. Moreover, under severe drought carboxylation efficiency of rubisco decreases and it acts more as oxygenase than carboxylase.

Under water deficit conditions other factors like abscisic acid (ABA) concentration and deficiencies of essential nutrients have also been shown to decrease stomatal conductance of leaves. Stomatal regulation is closely related to ABA concentrations in the leaves under water stress. Radin and Ackerson (1981) observed that during drought stress stomatal conductance of cotton was sensitive to nitrogen deficiency. In phosphorus-deficient cotton plants similar results were obtained (Radin, 1984). Hydraulic conductivity of the soils also contributed to the higher photosynthetic rates as it allowed the plants to rehydrate at night time and enable photosynthetic system to work efficiently during the morning (Pettigrew, 2004).

Respiration: Respiration occurs in all organs; its regulation under drought is important to understand. Mitochondrial respiration plays an important role in determining the growth, functioning, development and survival of plants (Gifford, 2003). Despite the significance of respiration, studies about the impact of drought stress on respiration are limited (Ribas-Carbo *et al.*, 2005).

Under water deficit conditions rate of respiration depends upon age and type of plant tissue, genotype, growth stage, activity of respiratory enzymes, ATP demand and duration and severity of stress (Atkin and Macherel, 2009). Drought stress can decrease rate of leaf and root respiration for a short time (Byrle *et al.*, 2001). Wullschlegel and Oosterhuis (1990) reported that under mild water deficit stress cotton boll respiration remained unaffected and slight reduction was observed under severe stress conditions. However, according to Loka and Oosterhuis (2014) respiratory rates of water stressed plants were decreased by 39% than to control.

ATP content: ATPs are mainly produced through the processes of photophosphorylation of photosynthesis and glycolysis of respiration in chloroplasts and mitochondria, respectively (Raymond and Pradet, 1983). Under water deficit conditions ATPs show considerable variation in the tissues. Flexas and Medrano (2002) reported that with decreasing relative water contents of leaves, leaf ATP content were also decreased. Lawlor and Tezara (2009) reported an increase in ATP content under mild water deficit conditions. Pandey *et al.* (2002) conducted experiments on cotton to investigate the production and concentration of different photosynthetic metabolites of leaves under drought conditions during the reproductive development and concluded that drought caused a decrease in ATP content of leaves, increase in concentration of nicotinamide adenine dinucleotide phosphate (NADP) while no significant change was recorded in pyruvate and 3-phosphoglyceric acid (3-PGA) contents of the leaves.

Oxidative damage: Inequality between light capture and utilization ability of plants under drought stress disturbs the leaf functioning. Production of various reactive oxygen species (ROS) like hydroxyl radicals (OH⁻), superoxide anion (O⁻²), hydrogen peroxide (H₂O₂) and singlet oxygen (O⁻¹) takes place due to inhibition of photosynthesis (Munne-Bosch and Penuelas, 2003). The production of reactive oxygen species is mainly because of decline in carbon dioxide (CO₂) fixation, resulting in escape of electrons towards oxygen (Foyer *et al.*, 1997)

Reactive oxygen species attack on various cell components like lipids and proteins and thus disturbing the normal activities of cells (Foyer *et al.*, 1997). Under drought stress organelles like mitochondria, chloroplasts and peroxisomes are mainly damaged by reactive oxygen species.

In chloroplast, excited pigments of thylakoid membranes react with O₂ to produce reactive oxygen species like hydrogen peroxide (H₂O₂) and hydroxyl radical (OH⁻) (Reddy *et al.*, 2004). The reaction of O₂ with reduced components of the electron transport chain in mitochondria and higher leakage of electrons in the matrix side of NADH dehydrogenase (Millar, 2001) and rubiquinone:cytochrome b resulted in production of reaction oxygen species (Nohl *et al.*, 2004).

Cotton Responses: Cotton can tolerate drought stress by a number of physiological, biochemical and molecular responses as shown in figure 2 (Oliveira *et al.*, 2013).

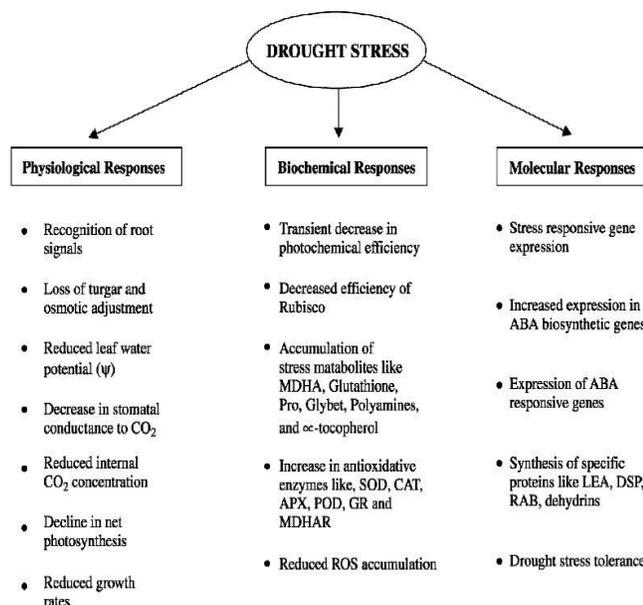


Figure 2. Different physiological, biochemical and molecular responses of drought stress on cotton.
Source: Oliveira *et al.* (2013).

Anti oxidant defense system: Oxidative stress in the plant can be minimized by antioxidant defense systems. In plants both enzymatic or non-enzymatic components constitute the antioxidant defense systems. Some important enzymes involved in antioxidant defense are catalase, superoxide dismutase and ascorbate peroxidase (Gaspar *et al.*, 2002). While flavonoids and polyamines (as non-enzymatic components) have been reported to contribute in providing the relief against oxidative damage (Bouchereau *et al.*, 1999). Xanthophyll-zeaxanthin cycle also provides protection to photosynthetic apparatus against radical injury. However, the response of antioxidants depends on the intensity and duration of drought stress and species involved (Reddy *et al.*, 2004).

To identify the changes in antioxidant system Mahan and Wanjura (2005) conducted experiments on field grown cotton under season long drought stress and observed slight change in glutathione metabolism in response to water deficit conditions and no major change in the levels of malondialdehyde (MDA). While activity of ascorbate peroxidase was less in control treatments as compared to drought affected plants. In potted grown cotton plants no significant change was observed in concentration of glutathione under drought stress, while levels of superoxide dismutase decreased in stressed plants than control (Kawakami *et al.*, 2010). However, activity of glutathione reductase in water stressed plants was significantly higher

with 94% more glutathione reductase in water stressed pistils than control (Loka and Oosterhuis, 2014). Sekmen *et al.* (2014) determined the level of lipid peroxidation in cotton in terms of thiobarbituric acid reactive substances (TBARS) and reported increase in TBARS under drought stress up to 169.4%. They further recorded increase in proline content, H_2O_2 content, SOD activity, CAT activity, POX activity, APX activity and NOX activity up to 30.9%, 248.03%, 70.69%, 37.9%, 43.2%, 22.4% and 26.8%, respectively in drought stressed cotton. However, NOX activity was increased by 26.8% under drought.

Aquaporins: Aquaporins are specific proteins that are embedded in the cell membrane and regulate the water movement across the plasma membrane. These are members of membrane proteins and are abundantly present in the plasma membrane and tonoplast (Tyerman *et al.*, 2002). In *Gossypium hirsutum* 71 members of aquaporins, (Park *et al.*, 2010) have been identified.

A gene GhPIP2;7 encoding the aquaporins in plasma membrane was found in cotton, and thought to be important for drought mitigation. Under water deficit conditions aquaporins increased the water permeability of the membrane by 10 to 20 folds (Maural and Chrispeels, 2001). Aquaporins are abundantly expressed in roots (Javot and Maurel, 2002) and thus play a vital role for water uptake by roots (Javot and Maurel, 2002) and osmoregulation of roots at cellular level (Javot *et al.*, 2003).

Proteins: Under environmental stresses synthesis of stress tolerant proteins is an important mechanism to tolerate adverse situations. Stress proteins are soluble in water and contribute towards stress tolerance by the hydration of cellular structures (Wahid and Close, 2007). Some important proteins produced under drought stress are heat shock proteins (HSPs) and late embryogenesis abundant (LEA) proteins which play an important role in drought tolerance of plants (Zhu *et al.*, 1997).

Heat shock proteins (HSPs): These are low-molecular-weight proteins produced in plants under unfavorable environmental conditions, mainly under drought and high temperature (Wahid and Close, 2007). Heat shock proteins are produced during the different growth stages of crop plants and help to prevent unfolding and denaturation of proteins, thus stabilize protein's structure (Gorantla *et al.*, 2006). They are responsible for stabilization and protection of mitochondria, chloroplasts, ribosomes etc.

Under drought or high temperature, dry land crops synthesize and accumulate higher levels of HSPs. Burke *et al.* (1985) planted cotton under water deficit conditions in field, where canopy temperature of 40°C was recorded due to deficit soil moisture. Production and accumulation of eight new polypeptides was reported in leaves of stressed cotton plants while no polypeptides were accumulated in leaves of control treatments. Sarwar *et al.* (2012) studied the behavior of 24 cotton genotypes under control vs drought conditions; all the

activities of nitrate and nitrite reductase were reduced however, there was substantial increase in number of total amino acids. Kuznetsov *et al.* (1999) reported accumulation of greater quantities of HSPs in cotton plants treated with heat stress at flowering stage. Additionally, osmotic adjustments were also observed in response to heat shock proteins in cotton.

Late embryogenesis abundant (LEA) proteins: Another important type of protein found in a number of plant species under water deficit conditions is late embryogenesis abundant protein. They were first discovered in cotton seeds (Baker *et al.*, 1988). They have lower molecular weight (10 to 30 kDa) and play a defensive role against the detrimental effects of drought. LEA proteins are produced during different developmental stages of cotton plant with various expression levels. They accumulate in both vegetative and reproductive plant parts under drought stress (Bray *et al.*, 2000).

They protect other important proteins from denaturation and play important role in the confiscation of ions inside the cell that are accumulated under drought (Gorantla *et al.*, 2006).

Compatible solutes/osmolytes: Compatible solutes are organic compounds with low molecular weight, high solubility and harmless even in excessive amount. They participate in detoxification of reactive oxygen species, osmoregulation, stabilization of membrane structures and proteins and in this way protect the plants (Kanwal *et al.*, 2013). Under water stress, reactive oxygen species like superoxide and hydrogen peroxide are produced and decomposed by specific enzymes. However, there is no enzyme present to decompose different hydroxyl radicals. Some compatible solutes act as scavengers of hydroxyl radicals (Akashi *et al.*, 2001). It has been reported that hydroxyl radicals were decreased in tobacco plant due to higher concentration of proline (Hong *et al.*, 2000). Citrulline and mannitol reactivity against hydroxyl radicals is much higher compared to proline; citrulline can decompose all hydroxyl radical molecules at the site of formation (Akashi *et al.*, 2001).

Some organic compounds such as amino acids have been found to accumulate in plants under water stress and play an important role in osmotic adjustment of the cell. Parida *et al.* (2007) observed an increase in total free amino acids concentration in cotton and concluded that this may be one aspect for drought alleviation in cotton.

Turner *et al.* (1986) observed the different physiological and morphological responses of cotton for osmotic adjustment under water-deficit conditions and reported 0.1 MPa diurnal changes in osmotic adjustment. Plants were grown in a growth chamber under different water levels. Both leaves and roots exhibited a considerable adjustment in osmotic potential in response to water stress. The osmotic adjustment of leaves was 0.41 MPa compared to 0.19 MPa in the roots.

Drought Management in Cotton:

Breeding and genetics: To improve the water use efficiency

of plants, three main processes are included in breeding program: efficient uptake of available water, improving biomass production per unit water transpired and partitioning of produced biomass towards the economic parts (Condon *et al.*, 2004). Since cotton is native to regions frequently facing drought, substantial genetic variability exists against drought (Saranga *et al.*, 1998).

Drought tolerance is a polygenic trait (Ahmad *et al.*, 2009) and is correlated with various morphological and physiological characters (Singh, 2005) such as seedling vigor, root to shoot ratio, root system (Pace *et al.*, 1999), relative water content, excised leaf water loss, rate of transpiration and frequency and size of stomata, stomatal conductance, and rate of photosynthesis (Parida *et al.*, 2008).

Breeding programs related to drought tolerance mainly focus on choice of specific cotton varieties that yield well under water deficit conditions. Under such programs traits that can contribute towards drought mitigation are identified. Leaf and root characters (anatomical traits), stomatal and osmotic regulation (physiological traits) and measurement of plant water status (relative water contents, leaf osmotic potential and excised leaf water loss) are considered as important traits for cotton regarding this concern (Steel *et al.*, 2006; Basu *et al.*, 2007).

Qualitative trait loci (QTL) is the specific region of genes controlling a particular attribute/trait (Tanksley, 1997). Recent advances in molecular genetics enable the plant breeders to find out the sites on chromosomes having QTLs. The most sophisticated technique used for finding out QTLs important for drought tolerance is DNA marker technology (Prioul *et al.*, 1997).

Saranga *et al.* (2001) found 33 QTLs for five physiological variables and 46 QTLs for five measures of crop productivity in cotton when grown under drought conditions. Among physiological attributes, 11 QTLs were detected for osmotic potential and ratio of carbon isotopes, four for canopy temperature, three for chlorophyll a and four for chlorophyll b. For productivity traits, a total of 15, 13 and 10 QTLs were identified for boll weight, seed cotton yield and harvest index, respectively whereas four QTLs were reported each for dry matter and boll number.

Regulatory genes: It is a gene that is involved in the production of a substance that regulates the expression of one or more genes. Regulatory genes and their products are very important in stress tolerance in plants. Selvam *et al.* (2009) discovered a gene "KC3" considered important for drought tolerance. Various biochemical analyses confirmed that KC3 enhanced the drought tolerance efficiency of cotton. During severe deficit conditions, HSPCB genes become activated in cotton leaves which are responsible for peptide synthesis and help cotton plant to tolerate drought (Vloudakis *et al.*, 2002).

Osmoprotectants: Osmoprotectants play an important role in regulating the plant responses to multiple stresses, including drought stress. Important osmoprotectants in plants are

proline and glycinebetaine (Zhu, 2002). Foliar application of these osmoprotectants has been reported to alleviate drought stress in many crops including cotton (Makhdum *et al.*, 2006). They are involved in arbitrating osmotic adjustment and protecting membranes and sub cellular structures in drought stressed plants.

Drought tolerance ability of crop plants can be increased by spraying glycinebetaine (Raza *et al.*, 2014b). Glycinebetaine has been reported to improve the performance and yield of plants under drought stress (Chen *et al.*, 2000). Exogenously applied glycinebetaine mitigated drought (Hussain *et al.*, 2008) by maintaining plant water relations and photosynthetic rate because of regulation of stomata and improvement in Rubisco efficiency (Sakamoto and Murata, 2002).

Cotton accumulates higher amount of glycinebetaine than others crops (Blunden *et al.*, 2001). Meek *et al.* (1999) observed that glycinebetaine treated cotton plants had significantly higher boll number, stomatal conductance, number of effective sympodia and boll retention than untreated plants. Gorham and Jokinen (2011) stated that foliar application of glycinebetaine at the time of square formation enhanced the growth cotton when applied at 3 kg ha⁻¹. Sarwar *et al.* (2006) observed a positive relationship of glycinebetaine accumulation in cotton leaves with plant productivity under water stress environment. Similarly, Iqbal *et al.* (2006) reported that glycinebetaine significantly affected the number of bolls per plant, boll weight and seed cotton yield (Table 5).

Table 5. Effect of different doses of glycinebetaine on number of bolls per plant, boll weight and seed cotton yield.

Sr. #	Glycinebetaine dose (kg/ha)	No. of bolls per plant	Boll weight (g)	Seed cotton yield (kg/ha)
1	0.0	24	3.12	1965
2	1.0	25	3.29	2172
3	3.0	26	3.30	2252
4	6.0	27	3.30	2251
Significance at 0.01 probability		0.58**	0.05**	33.8**

Foliar application of potassium: Nutrients' elements availability is a basic necessity for plants' growth. Potassium (K) is one of the primary plant nutrients and plays an important role in stress tolerance of plants. Potassium is important for many plant processes like water relations, photosynthesis, translocation of photosynthates to various organs and activation of enzymes (Mengel and Kirkby, 2001). Spray of potassium under water deficit stress has been reported to help in enhancing the crop performance and ultimately yield (Raza *et al.*, 2013, 2014a).

There is evidence that plants have a larger internal requirement for K when suffering from environmental

stresses like drought (Cakmak and Engels, 1999). The reason for the increased requirement of potassium by plants when coped with environmental stresses is due to the fact that K is very important for CO₂ fixation and photosynthetic. Potassium also played protective role against the photooxidative damage to chloroplasts (Cakmak, 1997). Foliar applied potassium on drought stressed cotton improved lint yield, micronaire, fibre strength and fibre length compared to control (Ahmad *et al.*, 2013).

Many studies showed that the boll size, micronaire, and strength of cotton fiber was improved by potassium application. Various reports indicated that early maturity of cotton is required for adaptation to regions with short growing seasons, and it may be affected by foliar application of potassium (Gwathmey and Howard, 1998). Sawan *et al.* (2006) reported that various yield parameters like number of bolls per plant, boll weight, seed index, lint index, seed cotton yield, and lint yield per hectare was increased with foliar application of potassium.

Plant growth regulators: The concept of plant hormones was first defined in 1937 (Davies, 2010). Plant hormone is described as an endogenous organic compound synthesized in one part of a plant and translocated to targeted part, where it causes a physiological response. Phytohormones act as main signals during different stress conditions and almost all plant processes are directly or indirectly affected by phytohormones (Pospisilova *et al.*, 2005).

Some important plant hormones are auxins, salicylic acid, abscisic acid and ethylene (Gaspar *et al.*, 1996). Under water stress conditions, plant growth regulator treatments significantly increased water potential and improved chlorophyll content (Zhang *et al.*, 2004).

The foliar applied salicylic acid (SA) has been reported to improve yield of many crops including cotton (Makhdum *et al.*, 2006). Salicylic acid (SA) improves plant growth under water deficit conditions (Senaratna *et al.*, 2000). Under water deficit conditions foliar application of SA (100 ppm) and L-TRP (15 ppm) improved stomatal conductance and reduce water loss in cotton. Similarly, He *et al.* (2005) and Rao *et al.* (2012) reported that salicylic acid increased the efficiency of photosynthetic apparatus in cotton that produced more photosynthates.

Bouchereau *et al.* (1999) studied the levels of ethylene, abscisic acid (ABA) and indole-3-acetic acid (IAA) in cotton under water deficit conditions and reported that evolution of ethylene from bolls and abscisic acid content increased while concentrations of IAA decreased which resulted in boll abscission and ultimately yield reduction. Pandey *et al.* (2002) reported that ABA and ETH reduced the gas exchange parameters, Chl *a* and Chl *b* content.

Seagull and Giavalis (2004) observed significant increases in fiber production of cotton with exogenous application of indole-3-acetic acid compared to control. The highest value of lint yield was observed when applied at pre-anthesis stage.

The hormone treatments might induce cell division, resulting in more epidermal cells. While Chen and Guan (2011) observed improved yield and quality of cotton fiber with increasing auxins level at ovule and fiber development stage. Similarly, improvement in yield and quality of cotton was reported by over-expression of a gene responsible for the synthesis of the auxins indole-3-acetic acid (Chen and Guan, 2011).

Mulching: Mulching is the process of covering the soil surface with some material to make favorable conditions for plant growth, development and efficient crop production. Many organic and inorganic materials like crop residues, manures, papers, polyethylene compounds and chemicals are commonly used mulch materials to conserve water (Schahbazian and Nejad, 2006). For conserving soil and plant moisture mulching is considered as one of the important management practices. Water that evaporates from the soil under the mulch layer condenses on the lower surface of the sheet and goes back to the soil as droplets thus conserving soil moisture.

Higher yields of different crops were reported when grown with cover crops (a type of bio mulch) because of more infiltration of water into the soil, less water loss through evaporation and increased amount of organic matter into soil (Keith *et al.*, 1994). Robert *et al.* (2000) reported an increase of 35% lint yield in cotton plants grown in pots with wheat stubble mulch than in pots without stubbles and it was observed that mulched pots' plants showed higher values of water use efficiency than control treatments.

Polythene plastic mulch conserved more soil moisture than other mulches (Table 6) (Nasrullah *et al.*, 2011). Higher values of leaf area index, crop growth rate, 100 bolls weight, seed cotton yield, harvest index and water use efficiency was recorded in cotton when grown under plastic sheet mulch compared to other mulch treatment (ZongBin *et al.*, 2004; Shaozhong *et al.*, 2002; Nasrullah *et al.*, 2011).

Selection and use of proper mulch is one of new horizons of soil conservation and sustainable agriculture which should be studied in more depth to detect its short and long term impacts on arable lands (Schahbazian and Nejad, 2006).

Table 6. Impact of mulching material on growth and yield attributes of cotton.

Mulching, aterial	Plant height (cm)	Bolls per plant	100 Boll weight (g)	Seed cotton yield (kg/ha)
Cultural mulch	153.1ab	29.47a	318.2ab	2891b
Straw mulch	139.9c	22.78c	293.4c	2448d
Plastic mulch	155.5ab	30.62a	327.5a	3040a
Chemical mulch	146.9c	26.19b	304.8bc	2683c
LSD at 5%	7.35	1.40	14.84	136.60

Any of two means not having a common letter differ significantly at $p < 0.05$

Conclusion: Water deficit stress has detrimental effects on every growth and developmental stage of cotton. At early

growth stage, it causes smaller leaves due to less turgor, reduces plant height; under prolonged conditions production of smaller organs, hindered flower production and poor yield has also been observed. Reduction in yield is due to unequal distribution of assimilates. Following drought, disturbance in water relations and stomata closure results decrease in both photosynthesis and water-use efficiency. Production of reactive oxygen species in organelles like chloroplasts, mitochondria and peroxisomes is one of the major factors responsible for impaired cotton growth and productivity under drought stress. Drought tolerance mechanism involves a number of physiological and biochemical responses like reduction in water loss by increasing stomatal resistance, increased water uptake by developing large and deep root systems, accumulation of osmolytes and osmoprotectant synthesis. Some important plant hormones like salicylic acid, cytokinins and abscisic acid play an important role in drought tolerance. Scavenging of reactive oxygen species by enzymatic and non-enzymatic systems, cell membrane stability, expression of aquaporins and production of stress proteins are also important mechanisms of drought tolerance. Drought stress can be managed by the development of most suitable plant genotypes, use of plant growth regulators, osmoprotectants, potassium and some other strategies like mulching.

REFERENCES

- Achard, P., H. Cheng, L. De Grauwe, J. Decat, H. Schoutteten, T. Moritz and N.P. Harberd. 2006. Integration of plant responses to environmentally activated phytohormonal signals. *Sci.* 311:91-94.
- Ahmad, R., R.G.M. Hurt, E.A. Waraich, M.Y. Ashraf and M. Hussain. 2013. Effect of supplemental foliar applied potassium on cotton (*Gossypium hirsutum* L.) yield and lint quality under drought stress. *Pak. J. Life Soc. Sci.* 11:154-164.
- Ahmad, R.T., T.A. Malik, I.A. Khan and M.J. Jaskani. 2009. Genetic analysis of some morpho-physiological traits related to drought stress. *Int. J. Agric. Bio.* 11:235-240.
- Ahmad, S., M.A.S. Raza, M.F. Saleem, S.S. Zahra, I.H. Khan, M. Ali, A.M. Shahid, R. Iqbal and M.S. Zaheer. 2015. Mulching strategies for weeds control and water conservation in cotton. *J. Agric. Biol. Sci.* 8:299-306.
- Akashi, K., C. Miyake and A. Yokota. 2001. Citrulline, a novel compatible solute in drought tolerant wild watermelon leaves, is an efficient hydroxyl radical scavenger. *FEBS Lett.* 508:438-442.
- Alves, A.A.C. and T.L. Setter. 2004. Response of cassava leaf area expansion to water deficit: Cell proliferation, cell expansion and delayed development. *Ann. Bot. (London)* 94:605-613.

- Ashraf, M.Y., A.R. Azmi, A.H. Khan, S.S.M. Naqvi and S.A. Ala. 1995. Effect of water stress on different enzymatic activities in wheat. *Acta Physiol. Plant.* 17:615-620.
- Atkin, O.K. and D. Macherel. 2009. The crucial role of plant mitochondria in orchestrating drought tolerance. *Ann. Bot.* 103:581-597.
- Aujla, M.S., H.S. Hind and G.S. Buttar. 2005. Cotton yield and water use efficiency at various levels of water and N through drip irrigation under two methods of planting. *Agric. Water Manag.* 71:167-17.
- Bacon, M.A. 2004. *Water use efficiency in plant biology.* Blackwell Publishing, Oxford.
- Baker, J., C. Steele and L. Dure. 1988. Sequence and characterization of 6 Leu proteins and their genes from cotton. *Plant Mol. Biol.* 11:277-291.
- Basal, H., N. Dagdelen, A. Unay and E. Yilmaz. 2009. Effects of deficit drip irrigation ratios on cotton (*Gossypium hirsutum* L.) yield and fibre quality. *J. Agron. Crop Sci.* 195:19-29.
- Basu, P.S., M. Ali and S.K. Chaturvedi. 2007. Osmotic adjustment increases water uptake, remobilization of assimilates and maintains photosynthesis in chickpea under drought. *Indian J. Exp. Biol.* 45:261-267.
- Bielorai, H., I. Vaisman and A. Feigin. 1984. Drip irrigation of cotton with treated municipal effluents: I. Yield response. *J. Environ. Qual.* 13:231-234.
- Blum, A. 2005. Drought resistance, water use efficiency, and yield potential: Are they compatible, dissonant or mutually exclusive? *Aus. J. Agric. Res.* 56:1159-1168.
- Blunden, G., A.V. Patal, N.J. Armstrong and J. Gorham. 2001. Betaine distribution in the Malvaceae. *Phytochem.* 58:451-454.
- Bouchereau, A., A. Aziz, F. Larher and J. Martin-tanguy. 1999. Polyamines and environmental challenges: recent development. *Plant Sci.* 140:103-125.
- Boyer, J.S. 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. *Plant Physiol.* 46:233-235.
- Boyer, J.S. 1982. Plant productivity and environment. *Sci.* 218:443-448.
- Bray, E.A.J., E. Bailey-Serres and E. Weretilnyk. 2000. Responses to abiotic stresses. pp. 1158-1176. In: Buchanan, W. Gruissem and R. Jones (ed.). *Biochemistry and molecular biology of plants.* American Society of Plant Physiologists, America. pp.1158-1176.
- Burke, J.J., J.L. Hatfield, R.R. Klein and J.E. Mullet. 1985. Accumulation of heat shock proteins in field grown soybean. *Plant Physiol.* 78:394-398.
- Byrle, D.R., T.J. Bouma, U. Hartmond and D.M. Eissenstat. 2001. Influence of temperature and soil drying on respiration of individual roots in citrus, integrating green observations into a predictive model for the field. *Plant Cell Environ.* 24:781-790.
- Cakmak, I. and C. Engels. 1999. Role of mineral nutrients in photosynthesis and yield formation. pp.141-168. In: Rengel, Zn mineral nutrition of crops: mechanisms and implications. The Haworth Press, New York, USA. pp.141-168.
- Cakmak, I. 1997. Role of potassium in protecting higher plants against photooxidative damage. pp. 345-352. In: Johnston, A.E. (ed.), Food security in the WANA region, the essential need for balanced fertilization, International Potash Institute, Switzerland. pp.345-352.
- Chaves, M.M. and M.M. Oliveira. 2004. Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. *J. Exp. Bot.* 55:365-384.
- Chen, W.P., P.H. Li and T.H.H. Chen. 2000. Glycinebetaine increases chilling tolerance and reduces chilling induced lipid peroxidation in (*Zea mays* L.). *Plant Cell Environ.* 23:609-618.
- Chen, Z.J. and X. Guan. 2011. Auxin boost for cotton. *Nature Biotechnol.* 29:407-409.
- Cock, C.G. and K.M. Elzik. 1993. Fruiting of cotton and lint yield of cotton cultivars under irrigated and non irrigated conditions. *Field Crops Res.* 33:411-421.
- Condon, A.G., R.A. Richards, G.J. Rebetzke and G.D. Farquhar. 2004. Breeding for high water use efficiency. *J. Exp. Bot.* 55:2447-2460.
- Cornic, G. and A. Massacci. 1996. Leaf photosynthesis under drought stress. pp.347-366. In: N.R. Baker (ed.). *Photosynthesis and Environment,* Kluwer Academic Publishers, Germany. pp.347-366.
- Davies, P.J. 2010. The pPlant Hormones: Their Nature, Occurrence, and Functions. p. 1-15. In: P. J. Davies (ed.) *Plant Hormones.* Springer, Netherlands. p.1-15.
- Dias, D.C.F.S. and J. Marcos Filho. 1996. Electrical conductivity tests to evaluate the vigor of soybean (*Glycine max* L.) Merrill) seeds. *Sci. Agri.* 53:31-42.
- Enahli, S. and H.J. Earl. 2005. Physiological limitations to photosynthetic carbon assimilation in cotton under water stress. *Crop Sci.* 45:2374-2382.
- Faizan ullah, A. Bano and A. Nosheen. 2012. Effects of plant growth regulators on growth and oil quality of canola (*Brassica napus* L.) under drought stress. *Pak. J. Bot.* 44:1873-1880.
- Farooq, M., S.M.A. Basra, A. Wahid, Z.A. Cheema, M.A. Cheema and A. Khaliq. 2008. Physiological role of exogenously applied glycinebetaine in improving drought tolerance of fine grain aromatic rice (*Oryza sativa* L.). *J. Agron. Crop Sci.* 194: 325-333.
- Ferreira, de B.C.A., F.M. Lamas, G.G. de Brito and A.L.D.C. Borin. 2013. Water deficit in cotton plant originated from seeds treated with growth regulators. 2013. *Agropec. Trop. Goiania.* 43:417-423.
- Flexas, J. and H. Medrano. 2002. Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited. *Ann. Bot.* 89:183-189.

- Flexas, J., J. Bota F. Loreto G. Cornic and T.D. Sharkey. 2004. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biol.* 6:269-279.
- Fortucci, P. 2002. The Contribution of Cotton to Economy and Food Security in developing countries. In: Note presented at the Conference "Cotton and Global Trade Negotiations" sponsored by the World Bank and ICAC. pp.8-9.
- Foyer, C.H., M. Lelandais and K.J. Kunert. 1997. Photooxidative stress in plants. *Plant Physiol.* 92:696-717.
- Fryxell, P.N. 1992. A revised taxonomic interpretation of *Gossypium hirsutum* L. (Malvaceae). *Rheedea.* 2:108-165.
- Gaspar, T., C. Kevers, C. Penei, H. Greppin, D.M. Reid and T. Thorpe. 1996. Plant hormones and plant growth regulators in plant tissue culture. *In vitro Cell Dev. Biol.* 32:272-289.
- Gerik, T.J., K.L. Faver, P.M. Thaxton and K.M. El-Zik. 1996. Late season water stress in cotton. Plant growth, water use and yield. *Crop Sci.* 36:914-921.
- Gifford, R.M. 2003. Plant respiration in productivity models: Conceptualization, representation and issues for global terrestrial carbon-cycle research. *Func. Plant Bio.* 30:171-186.
- Gorantla M., P.R. Babu, V.B.R. Lachagari, A.M.M. Reddy, R. Wusirika, J.L. Bennetzen and A. R. Reddy. 2006. Identification of stress-responsive genes in an indica rice (*Oryza sativa* L.) using ESTs generated from drought-stressed seedlings. *J. Exp. Bot.* 58:253-265.
- Gorham, J. and K. Jokinen. 2011. Glycinebetaine treatment improves cotton yields in field trials in Pakistan. *World Cotton Conference II, Athens, Greece.* pp.329.
- Gwathmey, C.O. and D.D. Howard. 1998. Potassium effects on canopy light interception and earliness of no-tillage cotton. *Agron. J.* 90:144-149.
- Haque, M.M., D.J. Mackill and K.T. Ingram. 1992. Inheritance of leaf epicuticular wax content in rice. *Crop Sci.* 32:865-868.
- He, Y., Y. Liu, W. Cao, M. Huai, B. Xu and B. Huang. 2005. Effects of salicylic acid on heat tolerance associated with antioxidant metabolism in Kentucky Bluegrass. *Amer. J. Crop Sci.* 45:988-995.
- Hearn, A.B. 1994. Water relationships in cotton. *Outlook in Agriculture.* 10:159-166.
- Henrique, C.S.G.M., R.L.A. Bruno, P.D. Fernandes, W.E. Pereira, L.H.G.M. Lima, M.M.A. Lima and M.S. Vidal. 2011. Germination of cotton cultivar seeds under water stress induced by polyethyleneglycol-6000. *Sci. Agric.* 2:221-233.
- Hongbo, S., L. ZongSuo and S. MingAn. 2005. Changes of anti-oxidative enzymes and MDA content under soil water deficits among 10 wheat (*Triticum aestivum* L.) genotypes at maturation stage. *Colloids and Surfaces B: Biointerfaces.* 45:7-13.
- Hong, Z., K. Lakkineni, Z. Zhang and D.P.S. Verma. 2000. Removal of feedback inhibition of 1-pyrroline-5-carboxylate synthetase results in increased proline accumulation and protection of plants from osmotic stress. *Plant Physiol.* 122:1129-1136.
- Hussein, F., M. Janat and A. Yakob. 2011. Assessment of yield and water use efficiency of drip-irrigated cotton (*Gossypium hirsutum* L.) as affected by deficit irrigation. *Turk.J. Agric. Fores.* 35:611-621.
- Hussain, M., M.A. Malik, M. Farooq, M.Y. Ashraf and M.A. Cheema. 2008. Improving Drought tolerance by exogenous application of glycine-betaine and salicylic acid in sunflower. *J. Agron. Crop Sci.* 194:193-199.
- Ihsanullah. 2009. Molecular genetic studies for drought tolerance in cotton. Ph.D. Thesis, Quaid-i-Azam Univ. Islamabad.
- Iqbal, N., M.Y. Ashraf, F. Javed, V. Martinez and K. Ahmad. 2006. Nitrate reduction and nutrient accumulation in wheat (*Triticum aestivum* L.) grown in soil salinization with four different salts. *J. Plant Nutr.* 29:409-421.
- Javot, H., V. Lauvergeat, V. Santoni, F. Martin-Laurent, J. Guclu, J. Vinh, J. Heyes, K.I. Franck, A.R. Schaffner, D. Bouchez and C. Maurel. 2003. Role of a single aquaporin isoform in root water uptake. *Plant Cell.* 15:509-522.
- Javot, H. and C. Maurel. 2002. The role of aquaporins in root water uptake. *Ann. Bot.* 90:301-313.
- Jones, H.G., T.J. Flowers and M.B. Jones. 1991. *Plants under stress: biochemistry, Physiology and Ecology and their application for plant improvement.* Cambridge University Press, New York.
- Kanwal, H., M. Ashraf and M. Hameed. 2013. Water relations and ionic composition in the seedlings of some newly developed and candidate cultivars of wheat (*Triticum aestivum* L.) under saline conditions. *Pak. J. Bot.* 45:1221-1227.
- Kawakami, E.M., D.M. Oosterhuis and J.L. Snider. 2010. Physiological effects of L- ethylcyclopropene on well-watered and water-stressed cotton plants. *J. Plant. Growth Regul.* 29:280-288.
- Keith, E., C. Johnny and B. Mike. 1994. Drought management for cotton production. Electronic publication number DRO-17, December, 1994. North Carolina cooperative extension service, North Carolina State University, Raleigh, North Carolina.
- Khan, A.H., S.M. Mujtaba and B. Khanzada. 1999. Response of growth, water relation and solute accumulation in wheat genotypes under water deficit. *Pak. J. Bot.* 31: 461-468.
- Kies, N. 1982. Some aspects of water relationships of an F1 interspecific hybrid and its parents. Ph.D. Dissertation. New Mexico State University, Las Cruces.

- Kramer, P.J. and J.S. Boyer. 1995. Water relations of plants and soils. Academic Press, San Diego.
- Krieg, D.R. 2000. Cotton water relations. pp. 7-15. In : D.M. Oosterhuis (ed). Proc. 2000 Cotton research meeting and summaries of cotton research. Arkansas agriculture experimental statistics special report. pp.7-15.
- Kuznetsov, V.V., V. Rakitin, and V.N. Zholkevich. 1999. Effects of preliminary heat shock treatment on accumulation of osmolytes and drought resistance in cotton plants during water deficiency. *Plant physiol.* 107:399-406.
- Larcher, W. 2000. Plant ecophysiology. RIMA, Sao Carlos, SP, Brazil. pp.531.
- Lawlor, D.W. and G. Cornic. 2002. Photosynthetic carbon assimilation and associate metabolism in relation to water deficits in higher plants. *Plant Cell Environ.* 25:275-294.
- Lawlor, D.W. and W. Tezara. 2009. Causes of decreased photosynthetic rate and metabolic capacity in water deficient leaf cells: a critical evaluation of mechanisms and integration of processes. *Ann. Bot.* 103:561-579.
- Leidi, E.O., M. Lopez, J. Gorham and J.C. Gutierrez. 1999. Variation in carbon isotope discrimination and other traits related to drought tolerance in upland cotton cultivars under dryland conditions. *Field Crops Res.* 61:109-123.
- Levitt, J. 1980. Responses of plants to environment. 2nd ed. Academic press, New York.
- Loka, D.A. and D.M. Oosterhuis. 2014. Water-deficit stress effects on pistil biochemistry and leaf physiology in cotton (*Gossypium hirsutum* L.). *South African J. Bot.* 93:131-136.
- Loveys, B.R., L.J. Atkinson, D.J. Sherlock, R.L. Roberts, A.H. Fitter and O.K. Atkin. 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast and slow growing plant species. *Global Change Bio.* 9:895-910.
- Ludlow, M.M. and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. *Adv. Agron.* 43:107-153.
- Mahajan, S. and N. Tuteja. 2005. Cold, salinity and drought stresses. *Arch. Biochem and Biophys.* 44:139-158.
- Mahan, J. and D. Wanjura. 2005. Seasonal patterns of glutathione and ascorbate metabolism in field-grown cotton under water stress. *Crop Sci.* 45:193-201.
- Makhdum, M.I., Shababuddin and F. Ahmad. 2006. Effect of exogenous application of glycinebetaine on water relations in cotton (*Gossypium hirsutum* L.) in aridisols. *J. Sci. Technol. University of Peshawar:* 30:11-14.
- Malik, T.A., Sana-ullah and S. Malik. 2006. Genetic linkage studies of drought tolerant and Agronomic traits in cotton. *Pak. J. Bot.* 38:1613-1619.
- Massacci, A., S.M. Nabiev, L. Petrosanti, S.K. Nematov, T.N. Chernikova, K. Thor and J. Leipner. 2008. Response of the photosynthetic apparatus of cotton (*Gossypium hirsutum* L.) to the onset of drought stress under field conditions studied by gas-exchange analysis and chlorophyll fluorescence imaging. *Plant Physiol. Biochem.* 46:189-195.
- Maural, C. and M.J. Chrispeels. 2001. Aquaporins. A molecular entry into plant water relations. *Plant Physiol.* 125:135-138.
- Meek, C.R., D.M. Oosterhuis and A.T. Steger. 1999. Drought tolerance and foliar spray of glycinebetaine. pp.559-561. Proceedings of Beltwide Cotton Conferences, National Cotton Council of America, Memphis, USA. pp.559-561.
- Mengel, K. and E.A. Kirkby. 2001. Principles of plant nutrition. 5th ed., Kluwer Academic Publishers, Dordrecht.
- Mert, M. 2005. Irrigation of cotton cultivars improves seed cotton yield, yield components and fiber properties in the Hatay Region, Turkey. *Acta Agr. Scand.* 55:44-50.
- Millar, A.H., L.J. Sweetlove, P. Giege and C.J. Leaver. 2001. Analysis of the Arabidopsis mitochondrial proteome. *Plant Physiol.* 127:1711-1727.
- Munne-Bosch, S. and J. Penuelas. 2003. Photo- and antioxidative protection during summer leaf senescence in *Pistacia lentiscus* L. grown under mediterranean field conditions. *Ann. Bot.* 92:385-391.
- Nakagawa, J. 1994. Seed vigour tests based on seedling characteristics. In: Vieira, p. 49-85.
- Nasrullah, M., M.B. Khan, R. Ahmad, S. Ahmad, M. Hanif and W. Nazeer. 2011. Sustainable cotton production and water economy through different planting methods and mulching techniques. *Pak. J. Bot.* 43:1971-1983.
- Noreen, S., H.R. Athar and M. Ashraf. 2013. Interactive effects of watering regimes and exogenously applied osmoprotectants on earliness indices and leaf area index. In: cotton (*Gossypium hirsutum* L.) crop. *Pak. J. Bot.* 45:1873-1881.
- Ober, E.S., M.L. Bloa, C.J.A. Clark, A. Royal, K.W. Jaggard and J.D. Pidgeon. 2005. Evaluation of physiological traits as indirect selection criteria for drought tolerance in sugar beet. *Field Crops Res.* 91:231-249.
- Okogbenin, E., I.J. Ekanayake and M.C.M. Porto. 2003. Genotypic variability in adaptation responses of selected clones of cassava to drought stress in the Sudan savanna zone of Nigeria. *J. Agron Crop Sci.* 189:376-389.
- Oliveira, A.B., N.L.M. Alencar and E.G. Filho. 2013. Responses of organisms to water stress. 321-322. In: S. Akinci (ed). Preto, Brazil. pp.321-322.
- Orgaz, F., L. Mateos, and E. Fereres. 1992. Season length and cultivar determine optimum evapotranspiration deficit in cotton. *J. Agron.* 84:700-706.
- Pace, P.F., H.T. Cralle, S.H.M. El-Halawany, J.Y. Cothren and S.A. Senseman. 1999. Drought-induced changes in shoot and root growth of young cotton plants. *J. Cotton Sci.* 3:183-187.

- Pandey, D.M., C.L. Goswami, B. Kumar and S. Jain. 2002. Effect of growth regulators on photosynthetic metabolites in cotton under water stress. *Plant Bio.* 45:445-448.
- Parida, A.K., V.S. Dagaonka, M.S. Phalak and L.P. Aurangabadkar. 2008. Differential responses of the enzymes involved in proline biosynthesis and degradation in drought tolerant and sensitive cotton genotypes during drought stress and recovery. *Acta Plant Physiol.* 30:619-627.
- Parida, A.K., S.D. Vipin, M.S. Phalak, G.V. Umalkar and L.P. Aurangabadkar. 2007. Alteration in photosynthesis pigments, protein and osmotic components in cotton genotypes subjected to short-term drought stress followed by recovery. *Plant Biotechnol. Rep.* 1:37-48.
- Park, W., B.E. Scheffler, P.J. Bauer and B.T. Campbell. 2010. Identification of the family of Aquaporin genes and their expression in upland cotton (*Gossypium hirsutum* L.). *BMC Plant Bio.* 10:142.
- Patil, M.D., D.P. Biradar, V.C. Patil and B.S. Janagoudar. 2011. Response of Cotton Genotypes to Drought Mitigation Practices. *American-Eurasian J. Agric. Environ. Sci.* 11:360-364.
- Pereira, J.R., P.D. Fernandes and N.E.M. Beltrão. 1998. Deterioration, hardening and abnormalities in seed and seedling of upland cotton (*Gossypium hirsutum* L.) genotypes under water stress. *Revista Brasileira de Engenharia Agricola e Ambiental.* 2:186-194.
- Pettigrew, W.T. 2004. Physiological consequences of moisture deficit stress in cotton. *Crop Sci.* 44:1265-1272.
- Pettigrew, W.T. 2005. Moisture deficit effects on cotton lint yield, yield components, and boll distribution. *J. Agron.* 96:377-383.
- Pospisilova, J., M. Vagner, J. Malbeck, A. Travnickova and P. Batkova. 2005. Interactions between abscisic acid and cytokinins during water stress and subsequent rehydration. *Bio. Plant.* 49:533-540.
- Prioul, J.L., S. Quarrie, M. Causse and D. De-Vienn, D. 1997. Dissecting complex physiological functions through the use of molecular quantitative genetics. *J. Exp. Bot.* 48:1151-1163.
- Quisenberry, J.E. and B.L. McMichael. 1991. Genetic variation among cotton germplasm for water-use efficiency. *Environ. Exp. Bot.* 31:453-460.
- Radin, J.W. and R.C. Ackerson. 1981. Water relations of cotton plants under nitrogendeficiency: III. Stomatal conductance, photosynthesis and abscisic acid accumulation during drought. *Plant Physiol.* 67:115-119.
- Radin, J.W. 1984. Stomatal responses to water stress and to abscisic acid in phosphorus deficient cotton plants. *Plant Physiol.* 76:392-394.
- Radin, J.W. 1992. Reconciling water-use efficiency of cotton in field and laboratory. *Crop Sci.* 32:13-18.
- Rahman, S., M.S. Shaheen, M. Rahman and T.A. Malik. 2000. Evaluation of excised leaf water loss and relative water content as screening techniques for breeding drought resistant wheat. *Pak. J. Bio. Sci.* 3: 663-665.
- Rahman, M., I. Ullah, M. Assraf, J. Stewart and Y. Zafar. 2008. Genotypic variation for drought tolerance in cotton. *Agron, Sustain. Develop.* 28:439-447.
- Rao, S.R., A. Qayyum, A. Razzaq, M. Ahmad, I. Mahmood and A. Sher. 2012. Role of foliar application of salicylic acid and l-tryptophan in drought tolerance of maize. *JAPS* 22:768-772.
- Rauf, M., M. Munir, M. Hassan, M. Ahmad and M. Afzal. 2007. Performance of wheat genotypes under osmotic stress at germination and early seedling growth stage. *African J. Biotechnol.* 6:14-20.
- Raymond, P. and A. Pradet. 1983. Adenine nucleotide ratios and adenylate energy charge in energy metabolism. *Ann. Rev. Plant Physiol.* 34:199-224.
- Raza, M.A.S., M.F. Saleem and I.H. Khan 2015. Combined application of glycinebetaine and potassium on the nutrient uptake performance of wheat under drought stress. *Pak. J. Agri. Sci.*, 52(1):19-26.
- Raza, M.A.S., M.F. Saleem, G.M. Shah, I.H. Khan and A. Raza. 2014a. Exogenous application of glycinebetaine and potassium for improving water relations and grain yield of wheat under drought. *J. Soil Sci. Plant Nutri.* 14:348-364.
- Raza, M.A.S., M.F. Saleem, M. Jamil and I.H. Khan. 2014b. Impact of foliar applied glycinebetaine on growth and physiology of wheat (*Triticum aestivum* L.) under drought conditions. *Pak. J. Agric. Sci.* 51:327-334.
- Raza, M.A.S., M.F. Saleem, G.M. Shah, M. Jamil and I.H. Khan. 2013. Potassium applied under drought improves physiological and nutrient uptake performances of wheat (*Triticum aestivum* L.). *J. Soil Sci. Plant Nutri.* 13:175-185.
- Raza, M.A.S., M.F. Saleem, I.H. Khan, M. Jamil, M. Ijaz and M.A. Khan. 2012a. Evaluating the drought stress tolerance efficiency of wheat (*Triticum aestivum* L.) cultivars. *Russian J. Agric. Socio-Econo. Sci.* 12:41-46.
- Raza, M.A.S., M.F. Saleem, M.Y. Ashraf, A. Ali and H.N. Asghar. 2012b. Glycinebetaine applied under drought improved the physiological efficiency of wheat (*Triticum aestivum* L.) plant. *Soil Environ.* 31:67-71.
- Raza, M.A.S., M.F. Saleem, S.A. Anjum, T. Khaliq and M.A. Wahid. 2012c. Foliar application of potassium under water deficit conditions improved the growth and yield of wheat (*Triticum aestivum* L.). *JAPS* 22:431-437.
- Reddell, D.L., J.F. Prochaska and A.J. Cudrak. 1987. Sequential water stress in cotton: a stress day index model. *American Society of Agriculture Engineers.* (87-2080):23.
- Reddy, A. R., K.V. Chaitanya and M. Vivekanandan. 2004. Drought-induced responses of photosynthesis and

- antioxidant metabolism in higher plants. *J. Plant Physiol.* 161:1189-1202.
- Ribas-Carbo, M., N.L. Taylor, L. Giles, S. Busquets, P.M. Finnegan, D.A. Day, H. Lambers, H. Medrano, J.A. Berry and J. Flexas. 2005. Effects of water stress on respiration of soybean leaves. *Plant Physiol.* 139:466-473.
- Richards, J.S., D.L. Russell, R.L. Robker, M. Dajee and T.N. Alliston. 1998. Molecular mechanisms of ovulation and luteinization. *Mol. Cell. Endocrinol.* 145:47-54.
- Richard, R.A. and J.B. Passioura. 1981. Seminal root morphology and water use of wheat. II. Genetic variation. *Crop Sci.* 21:253-255.
- Robert, J.L., R.L. Baumhardt, S.K. Hicks and J.L. Heilman. 2000. Soil and plant water evaporation from strip-tilled cotton: Measurement and Simulation. *Agron. J.* 86:987-994.
- Rosenthal, W. D., G.F. Arkin, P.E. Shouse and W.R. Jordan. 1987. Water deficit effects on transpiration and leaf growth. *Agron. J.* 79:1019-1026.
- Sadok, W., M.E. Gilbert, M.A.S. Raza and T.R. Sinclair. 2012. Basis of slow wilting phenotype in soybean PI 471938. *Crop Sci.* 52:1261-1262.
- Sakamoto, A. and N. Murata. 2002. The role of glycinebetaine in the protection of plants from stress: clues from transgenic plants. *Plant Cell Environ.* 25:163-171.
- Sanchez-Blanco, M.J., P. Rodríguez, M.A. Morales, M.F. Ortuno and A. Torrecillas. 2002. Comparative growth and water relation of *Cistus albidus* and *Cistus monspeliensis* plants during water deficit conditions and recovery. *Plant Sci.* 162:107-113.
- Sara, B. and K. Fatahi. 2013. Study of effects of end-season drought stress on biological yield and harvest index of irrigated barely lines in moderate regions of Kermanshah province. *Sci. Agric.* 1:70-75.
- Saranga, Y., M. Menz, C.H. Jiang, R.J. Wright, D. Yakir and A.H. Paterson. 2001. Genomic dissection of genotype \times environment interaction conferring adaptation of cotton to arid conditions. *Genome Res.* 11:1988-1995.
- Saranga, Y., N. Sass, Y. Tal and R. Yucha. 1998. Drought conditions induce mote formation in interspecific cotton hybrids. *Field Crops Res.* 55:225-234.
- Sarwar, M.K.S., I. Ullah, M. Rahman, M.Y. Ashraf and Y. Zafar. 2006. Glycinebetaine accumulation and its relation to yield and yield components in cotton genotypes grown under water deficit conditions. *Pak. J. Bot.* 38:1449-1456.
- Sarwar, M.K.S., M.Y. Ashraf, M. Rehman and Y. Zafar. 2012. Genetic variability in different biochemical traits and their relationship with yield and parameters of cotton cultivar grown under water stress conditions. *Pak. J. Bot.* 44:515-520.
- Sawan, Z. M., S.A. Hafez, A.E. Basyony and A.R. Alkassas. 2006. Cottonseed, protein, oil yields and oil properties as affected by nitrogen fertilization and foliar application of potassium and a plant growth retardant. *World J. Agric. Sci.* 2:56-65.
- Schahbazian, N. and H. Nejad. 2006. The effects of different mulch types and irrigation intervals on cotton yield. *Die Bodenkultur.* 57:765-766.
- Seagull, R.W. and S. Giavalis. 2004. Pre- and post-anthesis application of exogenous hormones alters fiber production in *Gossypium hirsutum* L. Cultivar Maxxa GTO. *J. Cotton Sci.* 8:105-111.
- Sekmen, A.H., R. Ozgur, B. Uzilday and I. Turkan. 2014. Reactive oxygen species scavenging capacities of cotton (*Gossypium hirsutum*) cultivars under combined drought and heat induced oxidative stress. *Environ. Exp. Bot.* 99:144-149.
- Sellin, A., L. Sack, E. Ounapuu and A. Karusion. 2011. Impact of light quality on leaf and shoot hydraulic properties: a case study in silver birch (*Betula pendula*). *Plant Cell Environ.* 34:1079-1087.
- Selote, D.S. and R. Khana-Chopra. 2004. Drought-induced spikelet sterility is associated with an inefficient antioxidant defence in rice plants. *Physiol. Plant.* 121:462-467.
- Selvam, J.N., N. Kumaraeadiabel, A. Gopikrishnan, B.K. Kumar, R. Ravikesavan and M.N. Boopathi. 2009. Identification of a novel drought tolerance gene in (*Gossypium hirsutum* L. cv KC3). *Biomet. Crop Sci.* 4:9-13.
- Senaratna T., D. Touchell, E. Bunn and K. Dixon. 2000. Acetyl salicylic acid (aspirin) and salicylic acid induce multiple stress tolerance in bean and tomato plants. *Plant Growth Reg.* 30:157-161.
- Shaozhong, K., L. Zhang, Y. Liang and H. Cai. 2002. Effects of limited irrigation on yield and water use efficiency of winter wheat on the loess Plateau of China. *ACIAR Monograph.* 84:105-116.
- Silva, A.E.C., M.A. Gore, P.A. Sanchez, A.N. French, D.J. Hunsaker and M.E. Salvucci. 2012. Decreased CO₂ availability and inactivation of Rubisco limit photosynthesis in cotton plants under heat and drought stress in the field. *Environ. Exp. Bot.* 83:1-11.
- Silva, V.G.D.F., A.P.D. Andrade, P.D. Fernandes, I.D.F.D. Silva, C.A. de Azevedo and J.S. Araujo. 2010. Productive characteristics and water use efficiency in cotton plants under different irrigation strategies. *Rev. Bras. Eng. Agric. Ambient* 14:451-457.
- Simonneau, T., R. Habib, J.P. Goutouly and J.G. Buguet . 1993. Diurnal changes in stem diameter depend upon variation in water content: Direct evidence from peach trees. *J. Exp. Bot.* 44:615-621.

- Sinclair, T.R. 2005. Theoretical analysis of soil and plant traits influencing daily plant water flux on drying soils. *J. Agron.* 97:1148–1152.
- Singh, P., 2005. *Cotton Breeding*, 2nd edition. Kalyani Publishers, New Dehli, India.
- Soomro, M.H., G.S. Markhand and B.A. Soomro. 2011. Screening Pakistani cotton for drought tolerance. 2011. *Pak. J. Bot.* 44:383-388.
- Steel, K.A., A.H. Price, H.E. Shashidhar and J.R. Witcombe. 2006. Marker-assisted selection to introgress rice QTLs controlling root traits into an Indian Upland rice variety. *Theor. Appl. Gene.* 112:208-221.
- Tanksley, S.D. 1997. Mapping polygenes. *Ann. Rev. Gene.* 27:205-233.
- Tezara, W., V.J. Mitchell, S.D. Driscoll and D.W. Lawlor. 1999. Water stress inhibits plant photo-synthesis by decreasing coupling factor and ATP. *Nature.* 401:914-917.
- Turner, N.C., A.B. Hearn, J.E. Begg and G.A. Constable. 1986. Cotton (*Gossypium hirsutum* L.); Physiological and morphological responses to water deficit and their relation to yield. *Field Crops Res.* 14:153-170.
- Tyerman S.D., C.M. Niemietz and H. Brameley. 2002. Plant aquaporins: multifunctional water and solute channels with expanding roles. *Plant Cell Environ.* 25:173-194.
- Ullah, I., M. Rehman, M. Ashraf and Y. Zafar. 2008. Genotypic variation for drought tolerance in cotton (*Gossypium hirsutum* L.): Leaf gas exchange and productivity. *Flora J.* 203:105-115.
- Unlu, M., R. Kanber, B. Kapur, S. Tekin and D.L. Koc. 2011. The crop water stress index (CWSI) for drip irrigated cotton in a semi arid region of Turkey. *African J. Biotechnol.* 10:2258-2273.
- Vloudakis, A.E., S.A. Kosmas, S. Tsakas, E. Eliopoulos, M. Loukas and K. Kosmidou. 2002. Expression of selected drought-related genes and physiological responses of Greek cotton varieties. *Funct. Plant Biol.* 29:1237-1245.
- Wahid, A. and T.J. Close. 2007. Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. *Biol. Plantarum.* 51:104-109.
- Warren, C.R., N.J. Livingston and D.H. Turpin. 2004. Water stress decreases the transfer conductance of drought. *Tree Physiol.* 24:971-979.
- Wullschleger, S.D. and D.M. Oosterhuis. 1990. Photosynthetic carbon production and use by developing cotton leaves and bolls. *Crop Sci.* 30:1259-1264.
- Yagmur, B., A. Gurel, Y. Oren, B. Izci, A. Edrevas, H. Hakerlerner, S. Hayta, H. Akdemir and L. Yildiz-aktas. 2014. Effects of different drought applications and potassium doses on cotton yield and fiber quality. *Res. J. Agric. Environ. Manag.* 3:60-67.
- Zhang, M., L. Duan, Z. Zhai, J. Li, X. Tian, B. Wang, Z. He and Z. Li. 2004. Effects of plant growth regulators on water deficit-induced yield loss in soybean, Proc. 4th International Crop Science Congress Brisbane, Australia.
- Zhu, J.K. 2002. Salt and drought stress signal transduction in plants. *Annual Rev. Plant Bio.* 53:247–273.
- Zhu, J., P.M. Hasegawa and R.A. Bressan. 1997. Molecular aspects of osmotic stress in plants. *Critical Rev. Plant Sci.* 16:253-277.
- ZongBin, M., L. Ling, F.W. Ping, X.D. Yi and Y.T.Gang. 2004. Effect of wheat straw mulching on soil temperature, moisture and growth and development of summer cotton. *J. Henan Agric. Univ.* 38: 379-383.