

Biological and Agricultural Sciences Research Journal eISSN: 2959-653X; pISSN: 2959-6521 www.basrj.com DOI: https://doi.org/10.54112/basrj.v2023i1.18 Biol. Agri. Sci. Res. J., Volume, 2: 18



**Review** Artilce

# AN OVERVIEW OF DROUGHT TOLERANCE CHARACTERS IN COTTON PLANT: INCREASING CROP YIELD WITH EVERY WATER DROP

# HARAIRA AA<sup>1</sup>, MAZHAR HSUD<sup>2</sup>, AHMAD A<sup>1</sup>, SHABBIR MS<sup>1</sup>, TAHIR AR<sup>1</sup>, ZULIFQAR W<sup>1\*</sup>

<sup>1</sup>Department of Plant Breeding and Genetics, University of Agriculture Faisalabad, Pakistan <sup>2</sup>Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan

\*Correspondence author email address: waseemaqib88@gmail.com

# (Received, 7th January 2023, Revised 24st July 2023, Published 28th July 2023)

Abstract Drought stress is a major factor limiting cotton productivity and quality worldwide. Understanding the physiological and inheritable mechanisms underpinning failure forbearance in cotton is essential for developing strategies to ameliorate cotton yield under water-limited conditions. This review paper summarizes recent advances in our understanding of the physiological and inheritable mechanisms contributing to failure forbearance in cotton. We punctuate cotton's crucial physiological and biochemical responses to failure stress, including changes in photosynthesis, water use effectiveness, and bibulous adaptation. We also review recent progress relating genes and molecular pathways involved in failure forbearance in cotton through transcriptomics and genome-wide association studies. Although significant progress has been made in relating genes and physiological mechanisms involved in cotton failure forbearance, important work remains to completely understand the complex relations between factory responses to failure stress and the inheritable factors that govern these responses. This review paper underscores the need for continued exploration of the physiological and inheritable mechanisms underpinning cotton failure forbearance and the development of new strategies for perfecting cotton productivity and sustainability under waterlimited conditions. Finally, we bandy implicit strategies for perfecting cotton failure forbearance through inheritable engineering, parentage, and agronomic practices. Overall, this review provides a comprehensive overview of the current knowledge on physiological and inheritable failure forbearance in cotton and identifies crucial exploration requirements and openings for unborn progress.

[Citation: Haraira, A.A., Mazhar, H.S.U.D., Ahmad, A., Shabbir, M.S., Tahir, A.R., Zulifqar, W. (2023). An overview of drought tolerance characters in cotton plant: increasing crop yield with every water drop. Biol. Agri. Sci. Res. J., **2023**: 18. doi: <u>https://doi.org/10.54112/basrj.v2023i1.18</u>]

Keywords: Drought stress, drought tolerance, cotton molecular genetic basis, Gossypium hirsutum

#### Introduction

Climate change is a global issue, and all the countries on earth have been affected by it to some extent. It has a direct effect on crop plants and causes issues like vield loss and food security problems; because of the increase in temperature, different abiotic stresses have hindered plants growth out of which drought stress is a prominent one (Fahad et al., 2013; Naeem et al., 2018). It depends on several factors like the distribution and amount of rainfall, evaporation rate and soil's ability to hold water in it (Ullah et al., 2019; Zhang et al., 2016a). An increase in temperature causes an increase in evaporation, which leads to drought stress, and crops like cotton are highly affected by it. According to report by (Comas et al., 2013), in USA, drought stress alone caused 67% reduction in cotton lint yield. It devastates the field crops, with abiotic stresses causing 73% decline in cotton production worldwide (Mahmood et al., 2019).

Drought and heat stress are the major issues being faced by cultivated crops.(Anwar et al., 2022). In recent years drought has attracted many geologists, ecologists, and environmentalists (Mishra and Singh, 2010).

Drought refers to the water shortage for a specific period which affects the crop production (Abdelraheem et al., 2019). Global study proposes an increase of 4–5.8 °C in air and surface temperatures for upcoming decades. From 1979 to 2003, an increase of 0.35 and 1.13 °C has been recorded, courtesy climate change (Khan et al., 2018). Cotton is the most important crop grown in 76 countries for its fiber. Drought can drastically affect cotton fiber quantitatively and qualitatively (Sekmen et al., 2014). It is necessary to study and identify all characteristics that can provide cotton plant with tolerance against drought stress. These can be used as markers in future



breeding programs(Quevedo et al., 2022). Drought stress affects plant growth by reducing photosynthesis and cell expansion. Cotton crop is very sensitive to abiotic stresses, and they mostly cause loss of cotton lint which is an important yield yield component of the cotton crop (Khan et al., 2017; Magwanga et al., 2018a). Countries like Pakistan are one of those countries which are adversely affected by climate change and high-temperature issues. Crops like cotton require an adequate amount of water to produce a good yield. Still, because of the insufficient water and high temperature, cotton crop is often affected by drought stress and ultimately causes yield loss (Nagamalla et al., 2021; Xiao et al., 2020). Because these issues are increasing day by day so, it is the need of the hour to produce environment friendly and stress tolerant cotton varieties to tackle the drought stress in a best possible manner. Under drought stress crop photosynthesis reduces by both stomatal and nonstomatal factors (Zahoor et al., 2017a).

Drought is a major abiotic stress affecting more than 40% of agricultural area. Reduced N assimilation has been observed in crop plants affected by drought stress (Zahoor et al., 2017c). Studies on cotton tolerance for abiotic stresses would help to increase cotton production and will produce great economic value. Drought affects cotton plant's both metabolic and biological pathways (Wang et al., 2013). Cotton growth is considered to be divided in five different stages as per irrigation requirements (Bauer et al., 2012). For germination on a plantation, irrigation is crucial. Drought stress has little effect from emergence to the first square. Still, the following two stages, such as first square to first flower and first flower to peak bloom, are extremely vulnerable to abiotic stress, particularly drought stress. (Bauer et al., 2012; Ul-Allah et al., 2021). At last stage i.e., peak bloom to first boll open, drought stress doesn't have much effect on cotton crop but can affect fiber quality (Hussain et al., 2020). Studies have revealed that cotton Photosystem II's quantum efficiency decreases under drought stress (Massacci et al., 2008). Due to drought, losses in the proportion of payment in cotton crop have been estimated as 40.8% (Saleem et al., 2016). Cotton is called as 'white gold' as it is cultivated for its excellent fiber, but cotton production has adversely been affected by the increase in heat and water deficit (Abdelmoghny et al., 2020). Cotton may be considered as a well adapted crop to high temperature and water deficit, but study reveals that temperature above optimum has negative effects on the yield and quality of fiber (Loka and Oosterhuis, 2020). The cotton crop's yield is a multi-factor trait that is primarily influenced by a variety of variables. The ability to withstand or tolerate abiotic stresses, particularly drought stress, is a more complex feature that largely depends on two physiological and environmental components. (Abdelmoghny et al., 2020; Sun et al., 2021). Therefore, in-depth knowledge of morpho-physiological process, genetic

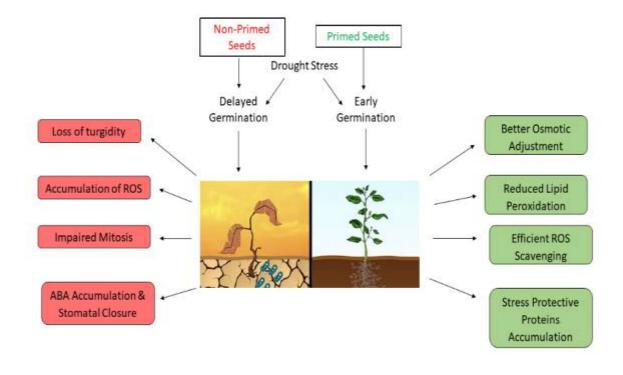
components and adaptive mechanisms against the cotton crop's drought is essential for a plant breeder to develop drought-tolerant varieties. Cotton plant, like many other plants adapts to the drought by producing HSPs. HSP are a group of gene products that help the plant by preventing protein denaturation (Maqbool et al., 2010). ABA hormone, is considered as the regulator of plant response to abiotic stresses, especially drought(Zhao et al., 2010). As different hormones perform different functions, thus collective application of different hormones can have synergistic and antagonistic effects (Hu et al., 2021; Mittal et al., 2014; Ullah et al., 2017). Many genes like overexpression of AtLOS5 increases the drought tolerance in cotton (Mazhar et al., 2023; Yue et al., 2012; Zahid et al., 2021). Study of genes of the cultivars that have previously been characterized for their drought tolerance provides framework for the breeding for drought tolerance (Cottee et al., 2013; Idbal et al., 2019). Drought tolerance is the ability of plant to prevent dehydration under water deficit conditions (Ilvas et al., 2020).

There are several traits that contribute towards drought tolerance i.e., stomatal size, stomatal number and osmotic adjustments etc. (Ahmad et al., 2009). Another mechanism that plant uses is the 'drought avoidance', it is continuation of plant physiological process even during drought (Ilyas et al., 2020; Manavalan et al., 2009). As the world population is increasing, demand for quality fiber is also increasing, but climate change is a strong challenge to meet the needs of growing human numbers (Esmaeili et al., 2020). Cotton genotypes, tolerant for heat and drought are pre-requisite for breeding programs. We need to identify genetic basis of all those morphological, physiological and biochemical traits that can contribute towards the tolerance in cotton against abiotic stresses (Saleem et al., 2021). (Qamer et al., 2021)

This study was concerned compile the published literature in recent years in a brief manner so that, in future, if a plant breeder wants to work on developing drought tolerant cotton varieties, he can have a thorough knowledge of the previous literature and save his time of searching and reading more than a ton a papers. This study includes several of morphological, physiological and biochemical traits that can contribute toward drought tolerance in cotton plant. In this review, we have also focused on the molecular approaches i.e., candidate genes for drought tolerance and QTLS identification. Despite the complexity of drought tolerance, a huge progress has been made to understand its mechanism. Several morpho-physiological and molecular adaptations can be helpful for breeder to develop a drought-tolerant cotton variety

# Drought stress and lint production

The complicated phenomena of lint production in cotton crops is under the control of several physiological processes and genes. Since cotton is an indeterminate crop and requires water continually for growth and output, water availability is the main factor influencing these physio-genetic processes. Effects of drought stress are mostly correlated with its duration, severity degree, and stage of plant growth. It results in the uptake of carbon and the buildup of biomass. (Zahoor et al., 2017b), decreased or sometimes no carbohydrate production (Galmés, Flexas, Savé, & Medrano, 2007), and reduced supplies to reproductive organs ultimately leads to small boll size (He et al., 2013) and reduction in lint yield (Figure. 1). Continuous increase in drought stress causes significant decrease in growth of the plant which ultimately reduces the final yield so, in cotton morpho-physiological play crucial role drought stress (Pettigrew, 2004).

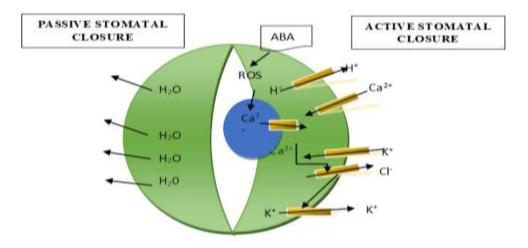


#### Figure 1: Difference between growth patterns of primed and non-primed seeds upon drought stress

# Morpho-Physiological Traits, contributing towards drought tolerance in cotton

the output. There are various morpho-physiological characteristics that cotton plants have that make them resistant to drought. (Pettigrew, 2004).

Continuously increasing drought stress results in a severe plant growth slowdown, ultimately lowering



## Roots

In the cotton plant, roots are the second-most significant vegetative organ after leaves. Due to their direct connection to soil water content and role as a supplier to other plant body parts, roots are the first organs to experience drought stress. Because it is challenging to examine roots from a dried soil, there is a dearth of data accessible for a thorough understanding of the mechanisms occurring in roots. The final output of the cotton crop is directly correlated with root growth. The amount of moisture available to roots influences the growth and development of upper plant body parts. (Zhang et al., 2017a). Soils with low water content mostly have longer plant roots and vice versa for soils with more water content (Hulugalle et al., 2015). Drought stress reduces plant growth by decreasing root mass and length densities. Plant breeders are more interested in rooting systems with many short and cylindrical roots because of their efficiency in response to drought stress. Sometimes a mild drought stress can trigger cotton plants to unlock their full yield potential (Niu et al., 2018). If plants have long and deeper roots, they can easily look for the moisture and nutrients from water (Luo et al., 2016).

# Leaves & Photosynthesis

Leaves are the most important organ of a plant in a battle with drought stress. Photosynthesis takes place in the leaves through which plants produce energy and food for themselves. When a plant faces drought stress, its stomata gets close, resulting in decreased rate of the photosynthesis process and decreased levels of  $CO_2$  in the leaves (Zhang et al., 2017b).Stomata are closed to inhibit water from going outside of the plant to tackle the water deficit hence cell activities are disturbed, a mild or drought stress for a short period can be tackled by a plant but prolong exposure to drought stress can severely effects plant. Response to drought to depends on its intensity and age of the cotton plant (Li et al., 2013). Up to 66% photosynthesis rate reduction was observed in mature leaves of a cotton plant as compared to its younger

leaves (Chastain et al., 2016).During drought stress plants usually adopt to various morphological phenomenon to tackle it i.e., accumulation of wax on leaves, rolling of leaves, thickening of cuticle, small leaves, tiny and dense number of stomata, and formation of vascular bundle sheath (Fang et al., 2015). Plants release heat using three major phenomena i.e., re-radiation, sensible heat loss and transcription. Transpiration is responsible for losing the most water contents from plants, i.e., up to 90% (Wan et al., 2009).Closing of stomata is the first step taken by plants to reduce water loss in unfavorable conditions. Stomatal conductance can be a possible morphological signal of drought tolerance induction (Figure. 2).

# Genetic basis of drought tolerance in cotton

Genes are the key regulators of the mechanisms that occur in living organisms. They are often termed as the key to start any biochemical reaction in the living organisms because these entities have all the information regarding growth and development of living beings. Not just in normal conditions, their role remains the same if any unwanted conditions suddenly develop. In case of drought stress, they also play a crucial role in survival of plants. Previously using bioinformatics studies, it was reported that some genes i.e., Gh-D01G0514 (Mehari et al., 2021), GhHDT4D (Zhang et al., 2020), GaNCED3a (Cai et al., 2021), StDREB2 (El-Esawi and Alayafi, 2019), GhTRX134 (Elasad et al., 2020), GhACX3 (Shiraku et al., 2021), ABP9 (Wang et al., 2017), GUSP1 (Hassan et al., 2021), GhJUB1L1 (Chen et al., 2021), LEA Protein (Magwanga et al., 2018c), Gh-D06G0281 (DTX) (Lu et al., 2019b), GhGA2ox1 (Shi et al., 2019), GhNAC79 (Guo et al., 2017), GhEXLB2 (Zhang et al., 2021), and Gh-A08G0694 (Shiraku et al., 2022) had upregulation in their expression when cotton plants are exposed to drought stress. Some gene functions are confirmed with the help of performed experiments; list of these genes given in the (Table. 1).

Gene	Specie	Function	Reference
GaTOP6B	Gossypium arboreum	Promotes Leaf and root development and act as a positive regulator in drought stress	(Shi et al., 2019)
GhSLAC1	Gossypium hirsutum	Controls Stomatal closure in drought stress.	(Ren et al., 2021)
GhGLK1	Gossypium	Controls leaf damage in drought stress	(Liu et al., 2021a)
GhFAR3.1	hirsutum Gossypium	Increases wax content and on leaves and helps in	(Lu et al., 2021)
Gh-A08G1120	hirsutum Gossypium	retention of water under drought stress Increases plant tolerance ability against drought and	(Kirungu et al.,
GTOM1	hirsutum Gossypium	salt stress conditions Increases efficiency of cotton plants to tackle drought	2019) (Lu et al., 2019a)
	hirsutum	and cold stress	

Table. 1: Candidate genes for drought tolerance in cotton

Cot-AD24498	Gossypium	Promotes root growth and help plants in tackling	
	hirsutum	drought stress	2018b)
Ac1-SST	Gossypium	Increase photosynthesis rate and plant de under	(Liu et al., 2021b)
	hirsutum	drought stress	

#### Transcription factors and other candidate genes

Proteins known as transcription factors have unique qualities and capabilities not present in other proteins. They typically cooperate in networks or pairs to modify particular regulatory pathways. They attach directly to the DNA, while some also use ligands. There are a lot of insightful facts about TFs for drought resistance in cotton crops that can be applied to new developments (Table. 2).

 Table. 2: Various transcription factors found in Cotton crop and their function

TF/Gene	Primer Sequences	Function	Reference	
HSP101	FP: GGAAGTGGAATCTGCGATAGT	NAC protein	(Yoshida et al.,	
	<b>RP: GATTTTGTCCCACCACTCTTTG</b>		2011)	
HSP3	FP: AGAAAAGTTGACCCTGACCGC		(Zhang et al., 2016b)	
	RP: AACCTCCTCTTCGAGACCAAAC			
HSC70	FP: TTGTTACCGTCCCTGCATACTT		(Qi et al., 2011)	
	<b>RP: GACATCAAAAGTACCGCCACC</b>			
GhNAC2	FP: ATGTGCATCGCAGTCCATC		(Gunapati et al.,	
	<b>RP: CTCCGTACAACGCCAAATCT</b>		2016)	
GbMYB5	FP: GACATCAATGGTTCAAAAGACAGC MYB protein		Chen et al., 2015	
	RP: ATTGAAGAACAGAAGTTGAATCCC			
GhWRKY41	FP: CTTACAGTGGAAGGAAAGAAGA WRKY protein		Chu et al., 2015	
	RP: TGAAATGAAAGGGAGATGTATTGT			
GhMKK1	FP: GAAGAAGAAGCAAAACCTCAGATG	: GAAGAAGAAGCAAAACCTCAGATG MMK protein		
	<b>RP: GTCATCACTACAGCCGCTC</b>			
GhMKK3	FP: CTGCGTCGGATTGGGAAG		Wang et al., 2016	
	<b>RP: GAACTACTAACCTCAAGCGG</b>			
GhMPK2	FP: GGATCCCAGGAAAATGGCAACTCCAG	Mitogen	Zhang et al., 2011	
	RP: GAGCTCCAGTGGTAAGACAACATCGT	activated protein		
		kinase		
GhMPK17	FP: GTTGCAAGCATCCGTGGAACCAGAAT		Zhang et al., 2014	
	RP: TAAGACAGATTAAGAACCTCCAGAGG			

# Conclusion

Based on the research and analysis in this review paper, it is clear that cotton product failure is a significant limiting factor, and that mastering failure forbearance in this crop is essential for maintaining yields and enhancing global food security. Examining the state of our understanding of the physiological and inherited causes underlying failure In the subject of forbearance in cotton, the important factors that contribute to the factory's capacity to withstand water stress have been underlined. The intricacy of the inherited and molecular mechanisms involved, as well as the high expenses and length of time required for screening and selecting, are just a few of the significant obstacles and constraints in breeding failure-tolerant cotton varieties that the review has connected. Despite these obstacles, the review has also uncovered some promising directions for future research and invention in this area, such as the use of cutting-edge genomic tools and strategies to pinpoint key genes and molecular pathways linked

to failure forbearance as well as the creation of more efficient and affordable webbing designs for tying failure-tolerant cotton lines together. Overall, this review has provided insightful information. into the physiological and inheritable base of failure forbearance in cotton crop, and has stressed the significance of continued exploration and development sweats in this area. By perfecting our understanding of the complex mechanisms involved in failure forbearance in cotton, we can develop new kinds that are more suitable to repel water stress and insure a more sustainable and flexible future for cotton product. **Declarations** 

#### **Conflict of interest**

The authors have no conflict of interest.

### Data Availability statement

All data generated or analyzed during the study are included in the manuscript.

**Ethics approval and consent to participate** Not applicable Consent for publication Not applicable Funding Not applicable Author Contributions

All authors contributed equally in this study.

### References

- Abdelmoghny, A. M., Raghavendra, K. P., Sheeba, J. A., Santosh, H. B., Meshram, J. H., Singh, S. B., Kranthi, K. R., and Waghmare, V. N. (2020). Morpho-physiological and molecular characterization of drought tolerance traits in Gossypium hirsutum genotypes under drought stress. *Physiol Mol Biol Plants* 26, 2339-2353. doi:10.1007/s12298-020-00890-3
- Abdelraheem, A., Esmaeili, N., O'Connell, M., Zhang, J. J. I. C., and Products (2019).Progress and perspective on drought and salt stress tolerance in cotton. 130, 118-129.
- Ahmad, R. T., Malik, T. A., Khan, I. A., and Jaskani, M. J. J. I. J. A. B. (2009). Genetic analysis of some morpho-physiological traits related to drought stress in cotton (Gossypium hirsutum). **11**, 235-240.
- Anwar, M., Saleem, M. A., Dan, M., Malik, W., Ul-Allah, S., Ahmad, M. Q., Qayyum, A., Amjid, M. W., Zia, Z. U., Afzal, H., Asif, M., Ur Rahman, M. A., and Hu, Z. (2022). Morphological, physiological and molecular assessment of cotton for drought tolerance under field conditions. *Saudi J Biol Sci* 29, 444-452. doi:10.1016/j.sjbs.2021.09.009
- Bauer, P., Faircloth, W., Rowland, D., Ritchie, G., Perry, C., and Barnes, E. J. C. i. m. f. h. r. C.
  C. I. (2012). Water-sensitivity of cotton growth stages. 1, 17-20.
- Cai, X., Jiang, Z., Tang, L., Zhang, S., Li, X., Wang, H., Liu, C., Chi, J., Zhang, X., and Zhang, J. (2021). Genome-wide characterization of carotenoid oxygenase gene family in three cotton species and functional identification of GaNCED3 in drought and salt stress. J Appl Genet 62, 527-543. doi:10.1007/s13353-021-00634-3
- Chastain, D. R., Snider, J. L., Choinski, J. S., Collins, G. D., Perry, C. D., Whitaker, J., Grey, T. L., Sorensen, R. B., van Iersel, M., Byrd, S. A., and Porter, W. (2016). Leaf ontogeny strongly influences photosynthetic tolerance to drought and high temperature in Gossypium hirsutum. *Journal of Plant Physiology* **199**, 18-28. doi: 10.1016/j.jplph.2016.05.003
- Chen, Q., Bao, C., Xu, F., Ma, C., Huang, L., Guo, Q., and Luo, M. (2021). Silencing GhJUB1L1 (JUB1-like 1) reduces cotton (Gossypium hirsutum) drought tolerance. *PLoS One* **16**, e0259382. doi:10.1371/journal.pone.0259382
- Comas, L., Becker, S., Cruz, V. M., Byrne, P. F., and Dierig, D. A. (2013). Root traits contributing

to plant productivity under drought. **4**. doi:10.3389/fpls.2013.00442

- Cottee, N. S., Wilson, I. W., Tan, D. K. Y., and Bange, M. P. (2013). Understanding the molecular events underpinning cultivar differences in the physiological performance and heat tolerance of cotton (Gossypium hirsutum). *Funct Plant Biol* **41**, 56-67. doi:10.1071/FP13140
- El-Esawi, M. A., and Alayafi, A. A. (2019). Overexpression of StDREB2 Transcription Factor Enhances Drought Stress Tolerance in Cotton (Gossypium barbadense L.). *Genes* (*Basel*) **10**. doi:10.3390/genes10020142
- Elasad, M., Ahmad, A., Wang, H., Ma, L., Yu, S., and Wei, H. (2020). Overexpression of CDSP32 (GhTRX134) Cotton Gene Enhances Drought, Salt, and Oxidative Stress Tolerance in Arabidopsis. *Plants* (*Basel*) 9. doi:10.3390/plants9101388
- Esmaeili, N., Cai, Y., Tang, F., Zhu, X., Smith, J., Mishra, N., Hequet, E., Ritchie, G., Jones, D., Shen, G., Payton, P., and Zhang, H. (2020). Towards doubling fibre yield for cotton in the semiarid agricultural area by increasing tolerance to drought, heat and salinity simultaneously. *Plant Biotechnology Journal* **19**, 462-476. doi:10.1111/pbi.13476
- Fahad, S., Chen, Y., Saud, S., Wang, K., Xiong, D., Chen, C., Wu, C., Shah, F., Nie, L., and Huang, J. (2013). Ultraviolet radiation effect on photosynthetic pigments, biochemical attributes, antioxidant enzyme activity and hormonal contents of wheat. *Food, Agriculture* and Environment 11.
- Fang, Y., Liao, K., Du, H., Xu, Y., Song, H., Li, X., and Xiong, L. (2015). A stress-responsive NAC transcription factor SNAC3 confers heat and drought tolerance through modulation of reactive oxygen species in rice. *Journal of Experimental Botany* 66, 6803-6817. doi:10.1093/jxb/erv386
- Gunapati, S., Naresh, R., Ranjan, S., Nigam, D., Hans,
  A., Verma, P. C., Gadre, R., Pathre, U. V.,
  Sane, A. P., and Sane, V. A. J. S. r. (2016).
  Expression of GhNAC2 from G. herbaceum,
  improves root growth and imparts tolerance to
  drought in transgenic cotton and Arabidopsis.
  6, 1-14.
- Guo, Y., Pang, C., Jia, X., Ma, Q., Dou, L., Zhao, F., Gu, L., Wei, H., Wang, H., Fan, S., Su, J., and Yu, S. (2017). An NAM Domain Gene, GhNAC79, Improves Resistance to Drought Stress in Upland Cotton. *Front Plant Sci* 8, 1657. doi:10.3389/fpls.2017.01657
- Hassan, S., Ahmad, A., Batool, F., Rashid, B., and Husnain, T. (2021). Genetic modification of Gossypium arboreum universal stress protein (GUSP1) improves drought tolerance in transgenic cotton (Gossypium hirsutum).

*Physiol Mol Biol Plants* **27**, 1779-1794. doi:10.1007/s12298-021-01048-5

- He, L., Yang, X., Wang, L., Zhu, L., Zhou, T., Deng, J., and Zhang, X. (2013). Molecular cloning and functional characterization of a novel cotton CBL-interacting protein kinase gene (GhCIPK6) reveals its involvement in multiple abiotic stress tolerance in transgenic plants. *Biochemical and Biophysical Research Communications* 435, 209-215. doi:https://doi.org/10.1016/j.bbrc.2013.04.080
- Hu, W., Zhang, J., Yan, K., Zhou, Z., Zhao, W., Zhang, X., Pu, Y., and Yu, R. (2021). Beneficial effects of abscisic acid and melatonin in overcoming drought stress in cotton (Gossypium hirsutum L.). *Physiol Plant* 173, 2041-2054. doi:10.1111/ppl.13550
- Hulugalle, N. R., Broughton, K. J., and Tan, D. K. Y. (2015). Fine root production and mortality in irrigated cotton, maize and sorghum sown in vertisols of northern New South Wales, Australia. Soil and Tillage Research 146, 313-322.
- doi:https://doi.org/10.1016/j.still.2014.10.004 Hussain, S., Ahmad, A., Wajid, A., Khaliq, T.,
- Hussain, N., Mubeen, M., Farid, H. U., Imran, M., Hammad, H. M., and Awais, M. (2020). Irrigation scheduling for cotton cultivation. *In* "Cotton production and uses", pp. 59-80. Springer.
- Ilyas, M., Nisar, M., Khan, N., Hazrat, A., Khan, A. H., Hayat, K., Fahad, S., Khan, A., and Ullah, A. (2020). Drought Tolerance Strategies in Plants: A Mechanistic Approach. *Journal of Plant Growth Regulation* **40**, 926-944. doi:10.1007/s00344-020-10174-5
- Iqbal, M., Khan, M. A., Chattha, W. S., Abdullah, K., and Majeed, A. (2019). Comparative evaluation of Gossypium arboreum L. and Gossypium hirsutum L. genotypes for drought tolerance. *Plant Genetic Resources: Characterization and Utilization* **17**, 506-513. doi:10.1017/s1479262119000340
- Khan, A., Pan, X., Najeeb, U., Tan, D. K. Y., Fahad, S., Zahoor, R., and Luo, H. (2018). Coping with drought: stress and adaptive mechanisms, and management through cultural and molecular alternatives in cotton as vital constituents for plant stress resilience and fitness. *Biol Res* **51**, 47. doi:10.1186/s40659-018-0198-z
- Khan, A., Tan, D. K. Y., Afridi, M. Z., Luo, H., Tung, S. A., Ajab, M., and Fahad, S. (2017). Nitrogen fertility and abiotic stresses management in cotton crop: a review. *Environmental Science* and Pollution Research 24, 14551-14566. doi:10.1007/s11356-017-8920-x
- Kirungu, J. N., Magwanga, R. O., Lu, P., Cai, X., Zhou, Z., Wang, X., Peng, R., Wang, K., and

Liu, F. (2019). Functional characterization of Gh\_A08G1120 (GH3.5) gene reveal their significant role in enhancing drought and salt stress tolerance in cotton. *BMC Genet* **20**, 62. doi:10.1186/s12863-019-0756-6

- Li, Y., Zhang, L., Wang, X., Zhang, W., Hao, L., Chu, X., and Guo, X. (2013). Cotton GhMPK6a negatively regulates osmotic tolerance and bacterial infection in transgenic Nicotiana benthamiana, and plays a pivotal role in development. *The FEBS Journal* **280**, 5128-5144.
  - doi:https://doi.org/10.1111/febs.12488
- Liu, J., Mehari, T. G., Xu, Y., Umer, M. J., Hou, Y., Wang, Y., Peng, R., Wang, K., Cai, X., Zhou, Z., and Liu, F. (2021a). GhGLK1 a Key Candidate Gene From GARP Family Enhances Cold and Drought Stress Tolerance in Cotton. *Front Plant Sci* 12, 759312. doi:10.3389/fpls.2021.759312
- Liu, R., Jiao, T., Zhang, Z., Yao, Z., Li, Z., Wang, S., Xin, H., Li, Y., Wang, A., and Zhu, J. (2021b). Ectopic Expression of the Allium cepa 1-SST Gene in Cotton Improves Drought Tolerance and Yield Under Drought Stress in the Field. *Front Plant Sci* 12, 783134. doi:10.3389/fpls.2021.783134
- Loka, D. A., and Oosterhuis, D. M. (2020). Physiological and Biochemical Responses of Two Cotton (Gossypium hirsutum L.) Cultivars Differing in Thermotolerance to High Night Temperatures during Anthesis. *Agriculture* 10 doi:10.3390/agriculture10090407
- Lu, P., Magwanga, R. O., Kirungu, J. N., Dong, Q., Cai, X., Zhou, Z., Wang, X., Xu, Y., Hou, Y., Peng, R., Wang, K., and Liu, F. (2019a). Genome-wide analysis of the cotton Gcoupled receptor proteins (GPCR) and functional analysis of GTOM1, a novel cotton GPCR gene under drought and cold stress. *BMC Genomics* 20, 651. doi:10.1186/s12864-019-5972-y
- Lu, P., Magwanga, R. O., Kirungu, J. N., Hu, Y., Dong, Q., Cai, X., Zhou, Z., Wang, X., Zhang, Z., Hou, Y., Wang, K., and Liu, F. (2019b). Overexpression of Cotton a DTX/MATE Gene Enhances Drought, Salt, and Cold Stress Tolerance in Transgenic Arabidopsis. *Front Plant* Sci 10, 299. doi:10.3389/fpls.2019.00299
- Lu, Y., Cheng, X., Jia, M., Zhang, X., Xue, F., Li, Y., Sun, J., and Liu, F. (2021). Silencing GhFAR3.1 reduces wax accumulation in cotton leaves and leads to increased susceptibility to drought stress. *Plant Direct* 5, e00313. doi:10.1002/pld3.313
- Luo, H. H., Zhang, Y. L., and Zhang, W. F. J. P. (2016). Effects of water stress and rewatering on photosynthesis, root activity, and yield of

cotton with drip irrigation under mulch. **54**, 65-73. doi:10.1007/s11099-015-0165-7

- Magwanga, R. O., Lu, P., Kirungu, J. N., Diouf, L., Dong, Q., Hu, Y., Cai, X., Xu, Y., Hou, Y., Zhou, Z., Wang, X., Wang, K., and Liu, F. (2018a). GBS Mapping and Analysis of Genes Conserved between Gossypium tomentosum and Gossypium hirsutum Cotton Cultivars that Respond to Drought Stress at the Seedling Stage of the BC<sub>2</sub>F<sub>2</sub> Generation. *Int J Mol Sci* **19**. doi:10.3390/ijms19061614
- Magwanga, R. O., Lu, P., Kirungu, J. N., Dong, Q., Hu, Y., Zhou, Z., Cai, X., Wang, X., Hou, Y., Wang, K., and Liu, F. (2018b). Cotton Late Embryogenesis Abundant (LEA2) Genes Promote Root Growth and Confer Drought Stress Tolerance in Transgenic Arabidopsis thaliana. *G3 (Bethesda)* 8, 2781-2803. doi:10.1534/g3.118.200423
- Magwanga, R. O., Lu, P., Kirungu, J. N., Lu, H., Wang, X., Cai, X., Zhou, Z., Zhang, Z., Salih, H., Wang, K., and Liu, F. (2018c). Characterization of the late embryogenesis abundant (LEA) proteins family and their role in drought stress tolerance in upland cotton. *BMC Genet* 19, 6. doi:10.1186/s12863-017-0596-1
- Mahmood, T., Khalid, S., Abdullah, M., Ahmed, Z., Shah, M. K. N., Ghafoor, A., and Du, X. (2019). Insights into Drought Stress Signaling in Plants and the Molecular Genetic Basis of Cotton Drought Tolerance. *Cells* 9. doi:10.3390/cells9010105
- Manavalan, L. P., Guttikonda, S. K., Phan Tran, L.-S., Nguyen, H. T. J. P., and physiology, c. (2009). Physiological and molecular approaches to improve drought resistance in soybean. 50, 1260-1276.
- Maqbool, A., Abbas, W., Rao, A. Q., Irfan, M., Zahur, M., Bakhsh, A., Riazuddin, S., and Husnain, T. (2010). Gossypium arboreum GHSP26 enhances drought tolerance in Gossypium hirsutum. *Biotechnol Prog* 26, 21-5. doi:10.1002/btpr.306
- Massacci, A., Nabiev, S. M., Pietrosanti, L., Nematov, S. K., Chernikova, T. N., Thor, K., and Leipner, J. (2008). Response of the photosynthetic apparatus of cotton (Gossypium hirsutum) to the onset of drought stress under field conditions studied by gasexchange analysis and chlorophyll fluorescence imaging. Plant Physiol Biochem 46, 189-95. doi:10.1016/j.plaphy.2007.10.006
- Mazhar, H. S., Shafiq, M., Ali, H., Ashfaq, M., Anwar, A., Tabassum, J., Ali, Q., Jilani, G., Awais, M., Sahu, R., and Javed, M. A. (2023). Genome-Wide Identification, and In-Silico Expression Analysis of YABBY Gene Family in Response to Biotic and Abiotic Stresses in

Potato (Solanum tuberosum). *Genes (Basel)* 14. doi:10.3390/genes14040824

- Mehari, T. G., Xu, Y., Magwanga, R. O., Umer, M. J., Shiraku, M. L., Hou, Y., Wang, Y., Wang, K., Cai, X., Zhou, Z., and Liu, F. (2021). Identification and functional characterization of Gh\_D01G0514 (GhNAC072) transcription factor in response to drought stress tolerance in cotton. *Plant Physiol Biochem* 166, 361-375. doi:10.1016/j.plaphy.2021.05.050
- Mishra, A. K., and Singh, V. P. J. J. o. h. (2010). A review of drought concepts. **391**, 202-216.
- Mittal, A., Gampala, S. S., Ritchie, G. L., Payton, P., Burke, J. J., and Rock, C. D. (2014). Related to ABA-Insensitive3(ABI3)/Viviparous1 and AtABI5 transcription factor coexpression in cotton enhances drought stress adaptation. *Plant Biotechnol J* 12, 578-89. doi:10.1111/pbi.12162
- Naeem, M., Naeem, M. S., Ahmad, R., Ihsan, M. Z., Ashraf, M. Y., Hussain, Y., and Fahad, S. (2018). Foliar calcium spray confers drought stress tolerance in maize via modulation of plant growth, water relations, proline content and hydrogen peroxide activity. *Archives of Agronomy and Soil Science* 64, 116-131. doi:10.1080/03650340.2017.1327713
- Nagamalla, S. S., Alaparthi, M. D., Mellacheruvu, S., Gundeti, R., Earrawandla, J. P. S., and Sagurthi, S. R. (2021). Morpho-Physiological and Proteomic Response of Bt-Cotton and Non-Bt Cotton to Drought Stress. *Front Plant Sci* **12**, 663576. doi:10.3389/fpls.2021.663576
- Niu, J., Zhang, S., Liu, S., Ma, H., Chen, J., Shen, Q., Ge, C., Zhang, X., Pang, C., and Zhao, X. (2018). The compensation effects of physiology and yield in cotton after drought stress. J Plant Physiol 224-225, 30-48. doi:10.1016/j.jplph.2018.03.001
- Pettigrew, W. T. (2004). Physiological Consequences of Moisture Deficit Stress in Cotton. *Crop Science* **44**, 1265-1272. doi:https://doi.org/10.2135/cropsci2004.1265
- Qamer, Z., Chaudhary, M. T., Du, X., Hinze, L., and Azhar, M. T. (2021). Review of oxidative stress and antioxidative defense mechanisms in Gossypium hirsutum L. in response to extreme abiotic conditions. *Journal of Cotton Research* **4**. doi:10.1186/s42397-021-00086-4
- Qi, Y., Wang, H., Zou, Y., Liu, C., Liu, Y., Wang, Y., and Zhang, W. J. F. L. (2011). Overexpression of mitochondrial heat shock protein 70 suppresses programmed cell death in rice. 585, 231-239.
- Quevedo, Y. M., Moreno, L. P., and BarragÁN, E. (2022). Predictive models of drought tolerance indices based on physiological, morphological and biochemical markers for the selection of cotton (Gossypium hirsutum L.) varieties.

*Journal of Integrative Agriculture* **21**, 1310-1320. doi:10.1016/s2095-3119(20)63596-1

- Ren, H., Su, Q., Hussain, J., Tang, S., Song, W., Sun, Y., Liu, H., and Qi, G. (2021). Slow anion channel GhSLAC1 is essential for stomatal closure in response to drought stress in cotton. *J Plant Physiol* **258-259**, 153360. doi:10.1016/j.jplph.2020.153360
- Saleem, M. A., Malik, W., Qayyum, A., Ul-Allah, S., Ahmad, M. Q., Afzal, H., Amjid, M. W., Ateeq, M. F., and Zia, Z. U. (2021). Impact of heat stress responsive factors on growth and physiology of cotton (Gossypium hirsutum L.). *Mol Biol Rep* 48, 1069-1079. doi:10.1007/s11033-021-06217-z
- Saleem, M. F., Sammar Raza, M. A., Ahmad, S., Khan, I. H., and Shahid, A. M. (2016). Understanding and Mitigating the Impacts of Drought Stress in Cotton- a Review. *Pakistan Journal of Agricultural Sciences*. doi:10.21162/pakjas/16.3341
- Sekmen, A. H., Ozgur, R., Uzilday, B., and Turkan, I. (2014). Reactive oxygen species scavenging capacities of cotton (Gossypium hirsutum) cultivars under combined drought and heat induced oxidative stress. *Environmental and Experimental Botany* 99, 141-149. doi:10.1016/j.envexpbot.2013.11.010
- Shi, J. B., Wang, N., Zhou, H., Xu, Q. H., and Yan, G. T. (2019). The role of gibberellin synthase gene GhGA20x1 in upland cotton (Gossypium hirsutum L.) responses to drought and salt stress. *Biotechnol Appl Biochem* 66, 298-308. doi:10.1002/bab.1725
- Shiraku, M. L., Magwanga, R. O., Cai, X., Kirungu, J. N., Xu, Y., Mehari, T. G., Hou, Y., Wang, Y., Agong, S. G., Peng, R., Wang, K., Zhou, Z., and Liu, F. (2021). Functional Characterization of GhACX3 Gene Reveals Its Significant Role in Enhancing Drought and Salt Stress Tolerance in Cotton. *Front Plant Sci* 12, 658755. doi:10.3389/fpls.2021.658755
- Shiraku, M. L., Magwanga, R. O., Zhang, Y., Hou, Y., Kirungu, J. N., Mehari, T. G., Xu, Y., Wang, Y., Wang, K., Cai, X., Zhou, Z., and Liu, F. (2022). Late embryogenesis abundant gene LEA3 (Gh\_A08G0694) enhances drought and salt stress tolerance in cotton. *Int J Biol Macromol* 207, 700-714. doi:10.1016/j.ijbiomac.2022.03.110
- Sun, F., Chen, Q., Chen, Q., Jiang, M., Gao, W., and Qu, Y. (2021). Screening of Key Drought Tolerance Indices for Cotton at the Flowering and Boll Setting Stage Using the Dimension Reduction Method. *Front Plant Sci* 12, 619926. doi:10.3389/fpls.2021.619926
- Ul-Allah, S., Rehman, A., Hussain, M., and Farooq, M. (2021). Fiber yield and quality in cotton under drought: Effects and management.

Haraira et al., (2023)

*Agricultural Water Management* **255**. doi:10.1016/j.agwat.2021.106994

- Ullah, A., Akbar, A., Luo, Q., Khan, A. H., Manghwar, H., Shaban, M., and Yang, X. (2019). Microbiome Diversity in Cotton Rhizosphere Under Normal and Drought Conditions. *Microb Ecol* **77**, 429-439. doi:10.1007/s00248-018-1260-7
- Ullah, A., Sun, H., Yang, X., and Zhang, X. (2017). Drought coping strategies in cotton: increased crop per drop. *Plant Biotechnol J* **15**, 271-284. doi:10.1111/pbi.12688
- Wan, J., Griffiths, R., Ying, J., McCourt, P., and Huang, Y. (2009). Development of Drought-Tolerant Canola (Brassica napus L.) through Genetic Modulation of ABA-mediated Stomatal Responses. Crop Science 49, 1539-1554.

doi:https://doi.org/10.2135/cropsci2008.09.05

- Wang, C., Lu, G., Hao, Y., Guo, H., Guo, Y., Zhao, J., and Cheng, H. (2017). ABP9, a maize bZIP transcription factor, enhances tolerance to salt and drought in transgenic cotton. *Planta* 246, 453-469. doi:10.1007/s00425-017-2704-x
- Wang, M., Wang, Q., and Zhang, B. (2013). Response of miRNAs and their targets to salt and drought stresses in cotton (Gossypium hirsutum L.). *Gene* 530, 26-32. doi:10.1016/j.gene.2013.08.009
- Xiao, S., Liu, L., Zhang, Y., Sun, H., Zhang, K., Bai, Z., Dong, H., Liu, Y., and Li, C. (2020). Tandem mass tag-based (TMT) quantitative proteomics analysis reveals the response of fine roots to drought stress in cotton (Gossypium hirsutum L.). *BMC Plant Biol* 20, 328. doi:10.1186/s12870-020-02531-z
- Yoshida, T., Ohama, N., Nakajima, J., Kidokoro, S., Mizoi, J., Nakashima, K., Maruyama, K., Kim, J.-M., Seki, M., Todaka, D. J. M. G., and Genomics (2011). Arabidopsis HsfA1 transcription factors function as the main positive regulators in heat shock-responsive gene expression. 286, 321-332.
- Yue, Y., Zhang, M., Zhang, J., Tian, X., Duan, L., and Li, Z. J. J. o. e. b. (2012). Overexpression of the AtLOS5 gene increased abscisic acid level and drought tolerance in transgenic cotton. 63, 3741-3748.
- Zahid, Z., Khan, M. K. R., Hameed, A., Akhtar, M., Ditta, A., Hassan, H. M., and Farid, G. (2021).
  Dissection of Drought Tolerance in Upland Cotton Through Morpho-Physiological and Biochemical Traits at Seedling Stage. *Front Plant* Sci 12, 627107. doi:10.3389/fpls.2021.627107
- Zahoor, R., Dong, H., Abid, M., Zhao, W., Wang, Y., and Zhou, Z. (2017a). Potassium fertilizer improves drought stress alleviation potential in cotton by enhancing photosynthesis and

carbohydrate metabolism. *Environmental and Experimental Botany* **137**, 73-83. doi:10.1016/j.envexpbot.2017.02.002

- Zahoor, R., Zhao, W., Abid, M., Dong, H., and Zhou, Z. (2017b). Title: Potassium application regulates nitrogen metabolism and osmotic adjustment in cotton (Gossypium hirsutum L.) functional leaf under drought stress. *Journal of Plant Physiology* **215**, 30-38. doi:https://doi.org/10.1016/j.jplph.2017.05.00
- Zahoor, R., Zhao, W., Abid, M., Dong, H., and Zhou, Z. (2017c). Title: Potassium application regulates nitrogen metabolism and osmotic adjustment in cotton (Gossypium hirsutum L.) functional leaf under drought stress. *J Plant Physiol* **215**, 30-38. doi:10.1016/j.jplph.2017.05.001
- Zhang, B., Chang, L., Sun, W., Ullah, A., and Yang, X. (2021). Overexpression of an expansin-like gene, GhEXLB2 enhanced drought tolerance in cotton. *Plant Physiol Biochem* **162**, 468-475. doi:10.1016/j.plaphy.2021.03.018
- Zhang, H., Khan, A., Tan, D. K. Y., and Luo, H. (2017a). Rational Water and Nitrogen Management Improves Root Growth, Increases Yield and Maintains Water Use Efficiency of Cotton under Mulch Drip Irrigation. *Frontiers in Plant Science* 8. https://doi.org/10.3389/fpls.2017.00912
- Zhang, H., Li, D., Zhou, Z., Zahoor, R., Chen, B., and Meng, Y. (2017b). Soil water and salt affect cotton (Gossypium hirsutum L.)



**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution, and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third-party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <u>http://creativecommons.org/licen</u> <u>ses/by/4.0/</u>. © The Author(s) 2023 photosynthesis, yield and fiber quality in coastal saline soil. *Agricultural Water Management* **187**, 112-121. doi:https://doi.org/10.1016/j.agwat.2017.03.0

- Zhang, H., Ni, Z., Chen, Q., Guo, Z., Gao, W., Su, X., and Qu, Y. (2016a). Proteomic responses of drought-tolerant and drought-sensitive cotton varieties to drought stress. *Mol Genet Genomics* 291, 1293-303. doi:10.1007/s00438-016-1188-x
- Zhang, J., Vibha, S., Stewart, J. M., and Underwood, J. J. J. O. C. S. (2016b). Heat-tolerance in cotton is correlated with induced overexpression of heat-shock factors, heatshock proteins, and general stress response genes. 20, 253-262.
- Zhang, J. B., He, S. P., Luo, J. W., Wang, X. P., Li, D. D., and Li, X. B. (2020). A histone deacetylase, GhHDT4D, is positively involved in cotton response to drought stress. *Plant Mol Biol* **104**, 67-79. doi:10.1007/s11103-020-01024-9
- Zhao, L., Hu, Y., Chong, K., and Wang, T. J. A. o. B. (2010). ARAG1, an ABA-responsive DREB gene, plays a role in seed germination and drought tolerance of rice. **105**, 401-409.