

## Recent Advances in Okra Responses to Drought

Xia An ✉, Xiahong Luo, Changli Chen, Tingting Liu, Wenlue Li, Lina Zou

Zhejiang Xiaoshan Institute of Cotton & Bast Fiber Crops, Zhejiang Institute of Landscape Plants and Flowers, Zhejiang Academy of Agricultural Sciences, Hangzhou, 311251, China

✉ Corresponding author email: [anxia@zaas.ac.cn](mailto:anxia@zaas.ac.cn)

Molecular Plant Breeding, 2022, Vol.13, No.26 doi: [10.5376/mpb.2022.13.0026](https://doi.org/10.5376/mpb.2022.13.0026)

Received: 03 Aug., 2022

Accepted: 30 Aug., 2022

Published: 29 Nov., 2022

**Copyright** © 2022 An et al., This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

### Preferred citation for this article:

An X., Luo X.H., Chen C.L., Liu T.T., Li W.L., and Zou L.N., 2022, Recent advances in okra responses to drought, Molecular Plant Breeding, 13(26): 1-6 (doi: [10.5376/mpb.2022.13.0026](https://doi.org/10.5376/mpb.2022.13.0026))

**Abstract** Drought is a major abiotic stress that can significantly affect seed germination, growth, flowering, and crop yield of okra. Under drought stress, okra plants actively reprogram the gene expression network and adjust the physiological metabolism to maintain growth and development. Characterizing the drought-induced changes at transcriptomic, physiological, and morphological levels should provide valuable information for selective breeding against drought. In this review, we summarize recent advances in drought response in okra and survey the molecular mechanisms underlying drought tolerance.

**Keywords** Okra; Drought; Metabolism; Drought resistance

## Background

Climate change and unsustainable farming make abiotic stresses including drought, high salinity, and extreme temperature more frequent (An et al., 2016; Zhu, 2016). Such adverse environmental factors inevitably limit the growth of plants and finally comprise the yield and quality of crops (Araus et al., 2002; Liu et al., 2014). Among them, drought has gained extensive attention due to its far-reaching impact on crop fitness and food security (An et al., 2020; Hu et al., 2006). Drought causes dramatic changes at the molecular, cellular, and physiological levels in plants (Lesk et al., 2016). For example, significant reprogramming of the transcriptome and proteome had been documented in plants under drought. Massive molecular changes could affect multiple cellular activities such as photosynthesis and dry matter accumulation in major crops including wheat and rice (Tabassum et al., 2017). At the physiological level, drought affects all stages of plant growth and development, leading to inhibition in plant growth and finally a reduction in yield. The severity of drought stress is only exacerbated by the shortage of water and inefficient water resource management globally. Thus, it is urgent to understand the mechanisms by which plants respond to drought (Zhang et al., 2018).

Okra (*Abelmoschus esculentus* L.) is an annual herb belonging to the Malvaceae family (Arapitsas, 2008). It is rich in protein, amino acids, dietary fiber, and other essential nutrients (Arapitsas, 2008). Along with its high adaptability to different environments, okra holds great economic value. Here, we summarized recent studies on the drought stress responses of okra to better understand the molecular basis underlying how okra copes with drought.

## 1 Morphological and Molecular Adaptations under Drought Stress

Plants keep a fine-tuned balance between the absorption and loss of water under normal growth conditions. However, such a balance is disrupted under drought, causing drastic changes in many aspects of plant physiology including plant morphology, reactive oxygen species (ROS) metabolism, stomatal movement, plant hormone regulation, photosynthesis, and biomass accumulation. We will focus on the morphological adaptation and the accumulation of protective proteins such as antioxidant enzymes under drought stress.

It is well-known that drought leads to changes in cellular structure and activity, which ultimately affect plant morphology. First, the leaf size is decreased to reduce transpiration under drought (Mahajan and Tuteja, 2005). Second, leaf senescence and defoliation are promoted by abscisic acid, jasmonic acid, and ethylene under drought

to reduce water loss (Mahajan and Tuteja, 2005). Moreover, the root system is usually enlarged due to enhanced division and elongation of root tip cells to promote water uptake (Bartels and Sunkar, 2005).

In addition to morphological adaptations, plants also upregulate the antioxidant defense system including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) to alleviate drought-induced oxidative stress.

Finally, plants have developed osmotic regulation as another adaptation mechanism, in which the accumulation of osmolytes can stabilize the structure and function of biological macromolecules by reducing the osmotic potential and maintaining the turgor pressure (Liu et al., 2014).

## 2 Drought-induce Cells Signaling

As drought could greatly hamper the growth and development of plants, plants have developed a sophisticated network to adapt and survive. Once the drought stress signal is perceived in plants, multiple signaling events are activated to promote or inhibit the expression of specific genes (Hu et al., 2006). These drought-responsive genes are divided into two main categories: genes for signaling such as transcriptional factors (TFs) and protein kinases (PKs) and genes that promote the production of osmolytes and antioxidant enzymes for protection against drought stress (Liu et al., 2014). Changes in the expression of these key genes lead to further changes in various physiological and biochemical processes, allowing adaptation and growth under drought (Hu et al., 2006).

TFs are essential for transcription initiation in eukaryotes including plants by binding to RNA polymerase II. Key TFs that are responsive to drought stress have been identified, including NAC, AP2, bZIP, MYB, and TFs with zinc finger domains (Hu et al., 2006; Liu et al., 2014; Zhu, 2002). For example, NAC was the first drought-responsive TF reported in *Arabidopsis* (Tran et al., 2004). In addition, zinc finger proteins positively regulate plant drought stress tolerance (Ben Saad et al., 2010; Luo et al., 2012). Interestingly, TFs could either positively or negatively regulate drought response. An example of a negative regulator is bZIP in rice and tobacco during drought stress (Huang et al., 2010; Liu et al., 2012). Finally, manipulating the expression of TFs could be used to enhance plant stress resistance. It has been demonstrated that alfalfa overexpressing *WXP1* (encoding a putative TF with an AP2 domain from *Medicago truncatula*) exhibited enhanced drought tolerance (Zhang et al., 2005).

Other drought-responsive genes enhance drought tolerance by promoting osmotic regulation. Osmotic regulation is mainly achieved by the accumulation of small molecule metabolites, which can adjust the osmotic pressure and reduce or even eliminate drought stress (Chen and Murata, 2002). Common osmolytes under drought include both inorganic ions mainly including  $K^+$ ,  $Na^+$ , and  $Ca^{2+}$  and metabolites such as proline (Liu et al., 2014). Consistent with the function of specific genes in promoting osmotic regulation, transgenic cotton plants overexpressing the rice *SNAC1* gene showed a higher level of proline and enhanced drought resistance compared to wild-type plants (Liu et al., 2014).

## 3 Impact of Drought on the Growth of Okra

Drought inhibits the growth and development of okra, leading to a decrease in the number of pods and yield. Chaturvedi et al. (2019) found that three developmental stages were most sensitive to drought stress: the vegetative stage, flowering stage, and post-podding stage. In the vegetative stage, active cell divisions allow plants to grow. Thus, drought stress at this stage shows an adverse impact on the overall development of the plants. In addition, okra is highly susceptible to drought stress during flowering, which could result in a smaller number of pods.

Drought-induced drop in okra yield is associated with poor transport of assimilated compounds, membrane damage, and altered physiological activities during the vegetative and flowering stages (Anjum et al., 2017). Since okra shows different susceptibility toward drought at distinct growth stages, the level of yield drop under drought is partially dependent on the timing of the stress. In addition, different cultivars exhibit a wide range of drought tolerance (Abd El-Fattah et al., 2019). Thus, the drought-induced drop in okra is also dependent on the cultivar (Razi et al., 2021).

## 4 Impact of Drought on Physiological Metabolisms in Okra

### 4.1 Impact of drought on membrane integrity in okra

Maintaining membrane integrity and stability under drought stress is the main manifestation of plant drought tolerance. However, an increased level of cell membrane damage and leaf temperature are observed under increasing severity of drought stress. Damage in the cell membrane further results in the leakage of water-soluble metabolites into the intercellular space, making electrical conductivity inversely proportional to the integrity of the membrane (Dasgan et al., 2019).

### 4.2 Impact of drought on osmolytes in okra

Drought-induced osmotic stress could inhibit cell division and is also involved in other processes such as stomatal conductance, photosynthesis, leaf water content, and growth. On the other hand, drought-induced accumulation of proline and total sugar could enhance the drought resistance of okra (Ali et al., 2022).

### 4.3 Impact of drought on the antioxidant defense system in okra

Drought can induce the generation of ROS, leading to oxidative stress in plants. To cope with the excessive ROS, a complex antioxidant defense system has been evolved in plants (Hu et al., 2006). For instance, an increase in the enzyme activity of ascorbate POD and CAT has been observed in okra under drought (Ali et al., 2022). Thus, increasing the capacity of the antioxidant defense system is one mechanism by which okra responds to drought.

### 4.4 Impact of drought on photosynthesis in okra

In the five okra cultivars tested, drought treatment resulted in a smaller leaf area compared to the controls (Sankar et al., 2008). In addition, Chaturvedi et al. (2019) showed a significant decrease in the photosynthesis rate in okra leaves under drought stress. Such a decrease can be largely attributed to a smaller leaf area, damage to the photosynthesis system, and the reduction of relative leaf water content (Chaturvedi et al., 2019).

## 5 Approaches to Enhance Drought Tolerance in Okra

There are several studies reporting approaches that can alleviate drought stress in okra. Ali et al. (2020) showed that foliar application of selenium can alleviate the drought-induced damages and improve the nutritional quality and yield of okra. El-Afifi et al. (2018) reported that spraying chitosan, glycine betaine, or silicon had an impact on the drought tolerance in okra. Interestingly, it was found that the alleviation of drought stress was associated with increased levels of vitamin C, carbohydrates, protein, and total sugar in okra siliques (El-Afifi et al., 2018). Pravisya et al. (2019) found that treating okra with *Pseudomonas fluorescens* (a rod-shaped bacterium) decreased drought-induced damages. The beneficial effect of bacterial treatment was associated with an enhancement in the activity of non-enzymatic antioxidants, relative water content, as well as contents of total sugar, free amino acids, and other metabolites (Pravisya et al., 2019).

## 6 Drought-induced Gene Expression in Okra

Currently, high-throughput sequencing has been widely used in plant transcriptomics to mine functional genes and to elucidate the genetic/evolutionary mechanisms in plant drought responses. For example, Shi et al. (2019) compared the transcriptomes of okra seedling leaves under different degrees of drought stress and found that the number of differentially expressed genes was positively associated with the severity of drought stress. As expected, drought caused reprogramming of the gene expression in multiple metabolic pathways. Remarkably, many TF genes including *bHLH*, *MYB*, *C2H2*, and *bZIP* were significantly up-regulated in okra seedlings under drought stress (Shi et al., 2019). Further investigation on these *TFs* may promise the generation of okra plants with enhanced drought resistance.

## 7 Perspectives

Despite recent studies on the drought response in okra, the molecular basis underlying drought tolerance remains elusive due to a lack of in-depth mechanistic investigations. This is in part because the okra genome is still unavailable, making the discovery and validation of drought-resistance genes difficult. On the other hand, research in okra, a non-model plant, is scarce with only a limited number of investigators. Nonetheless, the wide

application of multi-omics technologies (transcriptomics, proteomics, and metabolomics) may change the field drastically by unbiased identifying novel genes, proteins, and metabolites that are important in the drought response in okra.

### Authors' contributions

AX carried out the collection and analysis of relevant literature and drafted the manuscript. LXH participated in the analysis of the documents. CCL participated in the collation of the documents. LTT conceived of the study. LWL participated in its design. ZLN helped to draft the manuscript. All authors read and approved the final manuscript.

### Acknowledgements

This study was supported by the National Key R&D Program and Key Special Project of International Science and Technology Innovation Cooperation between Governments (2017YFE0195300), the Basic Public Welfare Research Program of Zhejiang Province (LGN20C150007), the National Natural Science Foundation of China (31801406; 31872130; 32202506), the China Agriculture Research System of MOF and MARA, China Agriculture Research System for Bast and Leaf Fiber Crops (CARS-16-S05), and the Water and Soil Health Discipline Integration Project of Zhejiang Academy of Agricultural Sciences. The authors would like to thank TopEdit ([www.topeditsci.com](http://www.topeditsci.com)) for its linguistic assistance during the preparation of this manuscript.

### References

- Abd El-Fattah B.E.S., Haridy A.G., and Abbas H.S., 2019, Response to planting date, stress tolerance and genetic diversity analysis among okra (*Abelmoschus esculentus* (L.) Moench.) varieties, *Genetic Resources and Crop Evolution*, 67(4): 831-851  
<https://doi.org/10.1007/s10722-019-00821-6>
- Ali J., Jan I., Ullah H., Ahmed N., Alam M., Ullah R., El-Sharnouby M., Kesba H., Shukry M., Sayed S., Nawaz T., 2022, Influence of Ascophyllum nodosum Extract Foliar Spray on the Physiological and Biochemical Attributes of Okra under Drought Stress, *Plants (Basel)*, 11(6): 790  
<https://doi.org/10.3390/plants11060790>  
PMid:35336672 PMCID:PMC8949179
- Ali J., Jan I.U., and Ullah H., 2020, Selenium Supplementation Affects Vegetative and Yield Attributes to Escalate Drought Tolerance in Okra, *Sarhad Journal of Agriculture*, 35  
<https://doi.org/10.17582/journal.sja/2020/36.1.120.129>
- An X., Jin G., Luo X., Chen C., Li W., and Zhu G., 2020, Transcriptome analysis and transcription factors responsive to drought stress in *Hibiscus cannabinus*, *PeerJ*, 8, e8470  
<https://doi.org/10.7717/peerj.8470>  
PMid:32140299 PMCID:PMC7047868
- An X., Zhang J., Dai L., Deng G., Liao Y., Liu L., Wang B., and Peng D., 2016, Isobaric Tags for Relative and Absolute Quantitation (iTRAQ)-Based Comparative Proteome Analysis of the Response of Ramie under Drought Stress, *International Journal of Molecular Sciences*, 17(10): 1607  
<https://doi.org/10.3390/ijms17101607>  
PMid:27689998 PMCID:PMC5085640
- Anjum S.A., Ashraf U., Zohaib A., Tanveer M., Naem M., Ali I., Tabassum T., and Nazir U., 2017, Growth and developmental responses of crop plants under drought stress: a review, *Zemdirbyste-Agriculture*, 104(3): 267-276  
<https://doi.org/10.13080/z-a.2017.104.034>
- Arapitsas P., 2008, Identification and quantification of polyphenolic compounds from okra seeds and skins, *Food Chemistry*, 110(4): 1041-1045  
<https://doi.org/10.1016/j.foodchem.2008.03.014>  
PMid:26047300
- Araus J.L., Slafer G.A., Reynolds M.P., and Royo C., 2002, Plant breeding and drought in C3 cereals: what should we breed for? *Annals of Botany*, 89(7): 925-940  
<https://doi.org/10.1093/aob/mcf049>  
PMid:12102518 PMCID:PMC4233799
- Bartels D., and Sunkar R., 2005, Drought and Salt Tolerance in Plants, *Critical Reviews in Plant Sciences*, 24(1): 23-58  
<https://doi.org/10.1080/07352680590910410>
- Ben Saad R., Zouari N., Ben Ramdhan W., Azaza J., Meynard D., Guiderdoni E., and Hassairi A., 2010, Improved drought and salt stress tolerance in transgenic tobacco overexpressing a novel A20/AN1 zinc-finger "AISAP" gene isolated from the halophyte grass *Aeluropus litoralis*, *Plant Molecular Biology*, 72(1): 171-190  
<https://doi.org/10.1007/s11103-009-9560-4>  
PMid:19838809
- Chaturvedi A.K., Surendran U., Gopinath G., Chandran K.M., Nk A., and Ct M.F., 2019, Elucidation of stage specific physiological sensitivity of okra to drought stress through leaf gas exchange, spectral indices, growth and yield parameters, *Agricultural Water Management*, 222: 92-104  
<https://doi.org/10.1016/j.agwat.2019.05.041>

- Chen T.H., and Murata N., 2002, Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes, *Current Opinion in Plant Biology*, 5(3): 250-257  
[https://doi.org/10.1016/S1369-5266\(02\)00255-8](https://doi.org/10.1016/S1369-5266(02)00255-8)
- Dasgan H.Y., Kucukkomurcu S., Aydoner Coban G., Kusvuran S., and Akhoundnejad Y., 2019, Screening of okra genotypes for their resistance to salinity and drought, *Acta Horticulture*, 1257: 95-102  
<https://doi.org/10.17660/ActaHortic.2019.1257.14>
- El-Afifi S., Ibrahim E., and Salem S., 2018, Effect of Water Stress and some Anti-Transpirants on Growth, Yield and Quality of Okra Plants (*Abelmoschus esculentus*), *Journal of Plant Production*, 9(7): 619-625  
<https://doi.org/10.21608/jpp.2018.36369>
- Hu H., Dai M., Yao J., Xiao B., Li X., Zhang Q., and Xiong L., 2006, Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice, *Proc Natl Acad Sci USA*, 103(35): 12987-12992  
<https://doi.org/10.1073/pnas.0604882103>  
PMid:16924117 PMCID:PMC1559740
- Huang X.S., Liu J.H., and Chen X.J., 2010, Overexpression of PtrABF gene, a bZIP transcription factor isolated from *Poncirus trifoliata*, enhances dehydration and drought tolerance in tobacco via scavenging ROS and modulating expression of stress-responsive genes, *BMC Plant Biology*, 10(1): 1-18  
<https://doi.org/10.1186/1471-2229-10-230>  
PMid:20973995 PMCID:PMC3017851
- Lesk C., Rowhani P., and Ramankutty N., 2016, Influence of extreme weather disasters on global crop production, *Nature*, 529(7584): 84-87  
<https://doi.org/10.1038/nature16467>  
PMid:26738594
- Liu C., Wu Y., and Wang X., 2012, bZIP transcription factor OsbZIP52/RISBZ5: a potential negative regulator of cold and drought stress response in rice, *Planta*, 235(6): 1157-1169  
<https://doi.org/10.1007/s00425-011-1564-z>  
PMid:22189955
- Liu G., Li X., Jin S., Liu X., Zhu L., Nie Y., and Zhang X., 2014, Overexpression of rice NAC gene *SNAC1* improves drought and salt tolerance by enhancing root development and reducing transpiration rate in transgenic cotton, *PLoS One*, 9(1): e86895  
<https://doi.org/10.1371/journal.pone.0086895>  
PMid:24489802 PMCID:PMC3904958
- Luo X., Bai X., Zhu D., Li Y., Ji W., Cai H., Wu J., Liu B., and Zhu Y., 2012, GsZFP1, a new Cys2/His2-type zinc-finger protein, is a positive regulator of plant tolerance to cold and drought stress, *Planta*, 235(6): 1141-1155  
<https://doi.org/10.1007/s00425-011-1563-0>  
PMid:22160567
- Mahajan S., and Tuteja N., 2005, Cold, salinity and drought stresses: an overview, *Arch Biochem Biophys*, 444(2): 139-158  
<https://doi.org/10.1016/j.abb.2005.10.018>  
PMid:16309626
- Pravisisya P., Jayaram K.M., and Yusuf A., 2019, Biotic priming with *Pseudomonas fluorescens* induce drought stress tolerance in *Abelmoschus esculentus* (L.) Moench (Okra), *Physiol Molecular Biology Plants*, 25(1): 101-112  
<https://doi.org/10.1007/s12298-018-0621-5>  
PMid:30804633 PMCID:PMC6352537
- Razi K., Bae D.W., and Muneer S., 2021, Target-Based Physiological Modulations and Chloroplast Proteome Reveals a Drought Resilient Rootstock in Okra (*Abelmoschus esculentus*) Genotypes, *International journal of molecular sciences*, 22(23): 12996  
<https://doi.org/10.3390/ijms222312996>  
PMid:34884801 PMCID:PMC8657999
- Sankar B., Jaleel C.A., Manivannan P., Kishorekumar A., Somasundaram R., and Panneerselvam R., 2008, Relative efficacy of water use in five varieties of *Abelmoschus esculentus* (L.) Moench. under water-limited conditions, *Colloids Surf B Biointerfaces*, 62(1): 125-129  
<https://doi.org/10.1016/j.colsurfb.2007.09.025>  
PMid:17988840
- Shi D., Wang J., Bai Y., and Liu Y., 2019, Transcriptome sequencing of okra (*Abelmoschus esculentus* L. Moench) uncovers differently expressed genes responding to drought stress, *Journal of Plant Biochemistry and Biotechnology*, 29(2): 155-170  
<https://doi.org/10.1007/s13562-019-00528-w>
- Tabassum T., Farooq M., Ahmad R., Zohaib A., and Wahid A., 2017, Seed priming and transgenerational drought memory improves tolerance against salt stress in bread wheat, *Plant Physiology Biochemistry*, 118, 362-369  
<https://doi.org/10.1016/j.plaphy.2017.07.007>  
PMid:28711787

- Tran L.S., Nakashima K., Sakuma Y., Simpson S.D., Fujita Y., Maruyama K., Fujita M., Seki M., Shinozaki K., and Yamaguchi-Shinozaki, K., 2004, Isolation and functional analysis of Arabidopsis stress-inducible NAC transcription factors that bind to a drought-responsive cis-element in the early responsive to dehydration stress 1 promoter, *Plant Cell*, 16, 2481-2498  
<https://doi.org/10.1105/tpc.104.022699>  
PMid:15319476 PMCid:PMC520947
- Zhang J.Y., Broeckling C.D., Blancaflor E.B., Sledge M.K., Sumner L.W., and Wang Z.Y., 2005, Overexpression of WXP1, a putative *Medicago truncatula* AP2 domain-containing transcription factor gene, increases cuticular wax accumulation and enhances drought tolerance in transgenic alfalfa (*Medicago sativa*), *Plant Journal*, 42(5): 689-707  
<https://doi.org/10.1111/j.1365-313X.2005.02405.x>  
PMid:15918883
- Zhang X., Lei L., Lai J., Zhao H., and Song W., 2018, Effects of drought stress and water recovery on physiological responses and gene expression in maize seedlings, *BMC Plant Biology*, 18(1): 68  
<https://doi.org/10.1186/s12870-018-1281-x>  
PMid:29685101 PMCid:PMC5913800
- Zhu J.K., 2002, Salt and drought stress signal transduction in plants, *Annual Review of Plant Biology*, 53: 247-273
- Zhu J.K., 2016, Abiotic Stress Signaling and Responses in Plants, *Cell*, 167(2): 313-324  
<https://doi.org/10.1016/j.cell.2016.08.029>  
PMid:27716505 PMCid:PMC5104190