



# Abiotic Stress Responses in Groundnut (*Arachis hypogaea* L.): Mechanisms and Adaptations

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M. K. Kalarani, A. Senthil, S. Punitha, S. Sowmyapriya, M. Umapathi, and V. Geethalakshmi

## Abstract

The world population is rising at a fast pace and may reach 6–9.3 billion by 2050, but food production is rapidly declining due to the detrimental effects of numerous environmental stresses. According to climate change predictions, extreme weather events will become more frequent in tropical and subtropical areas. Extreme weather events cause abiotic stresses such as water stress, temperature stress, radiation stress, and salt stress, all of which have a significant influence on the productivity of crops such as groundnut (*Arachis hypogaea* L.). Globally, groundnut is a significant oil and food crop, ranking third and fourth in terms of protein and edible oil, respectively. Recent advances in groundnut physiology, plant phenotyping, and genomics have resulted in new insights into the abiotic stress tolerance mechanisms in groundnut, providing breeders with a better understanding of the gene networks involved in stress tolerance as well as newer tools for genetic improvement of groundnut for higher yield under stress conditions. This chapter discusses the abiotic stresses that impact groundnut production, as well as recent advances in employing physiological and genetic methods to increase abiotic stress tolerance in groundnut.

M. K. Kalarani (✉) · A. Senthil · S. Punitha · S. Sowmyapriya  
Directorate of Crop Management, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India  
e-mail: [kalarani.mk@tnau.ac.in](mailto:kalarani.mk@tnau.ac.in)

M. Umapathi  
Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

V. Geethalakshmi  
Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

**Keywords**

Oil seed · Moisture stress · Antioxidants · Reactive oxygen species · Yield

**11.1 Introduction**

Next to soybean, groundnut (*Arachis hypogaea* L.) is the world's most important legume in terms of production and is often produced as a rain-fed crop. India is the world's second largest producer of groundnut (68.57 lakh tonnes), after China (166.24 lakh tonnes) (Groundnut Outlook 2018). The area under groundnut cultivation in India has decreased from 41.35 lakh ha in 2017–2018 to 40.12 lakh ha in 2018–2019 due to various reasons. Hence, both the production and yield decreased from 52.75 lakh tonnes and 1269 kg ha<sup>-1</sup> in 2017–2018 to 37.70 lakh tonnes and 931 kg ha<sup>-1</sup> in 2018–2019, respectively. Both biotic and abiotic stresses have contributed to groundnut's declining production and productivity in recent years, and among these, abiotic stresses have emerged as a major cause for this.

Among the abiotic stresses, drought, high-temperature, and salinity stresses are the significant abiotic factors that cause limitations to groundnut production. More than 70% of groundnut cultivation in Asia is in arid or semiarid regions, where the crop is subjected to drought regularly with varying intensity and duration and 15% of this land is also subject to salt stress (Reddy et al. 2003). Because it is a rain-fed crop, groundnut is particularly vulnerable to drought, which is brought on by climate change, which reduces yields dramatically. However, groundnut is a moderately salt-sensitive plant, but the amount of salinity of the soil or water might restrict the yield. Because of climate change and global warming, groundnut yields in India are expected to decline by 23–36% with a mean air temperature increase of 2–3 °C (Hoegh-Guldberg et al. 2018). High temperatures at crucial growth phases have an impact on the pod yield and also intensify the moisture stress, both of which contribute to additional yield losses (Prasad et al. 1999).

As the crop progresses throughout its life cycle, the plant's response to various environmental stresses will differ depending upon the genotype. The response to environmental stresses is more prominent at some phenological stages than at different phenophases. As a result, field tolerance of a genotype to any abiotic stress is assessed throughout multiple development stages. Several studies have found that the sensitivity of groundnut genotypes to abiotic stresses varies during the vegetative stage and pod growth stage, although the reproductive stage is more vulnerable to such challenges (Hamidou et al. 2013). There are just a few studies on screening groundnut genotypes for high-temperature and salt stress under controlled conditions and in the field conditions. To establish a breeding program and create better cultivars for abiotic stress environments, it is critical to know how plants respond under stress and in non-stress situations. This review addresses the groundnut plant's responses to numerous abiotic stresses, as well as the mechanism of tolerance and adaptability at various growth stages.

## 11.2 Abiotic Stress Responses in Groundnut

Abiotic stresses have different effects on plants, and the plants which have inherent tolerance strive to change their morphophysiological and biochemical characteristics to combat these stresses, whereas vulnerable plants acquire symptoms (Zafar et al. 2018) that lead to a reduction in growth and development.

### 11.2.1 Morphological Responses

Drought stress has a major influence on morphological characteristics, particularly the roots. The root is the plant's primary organ, which responds and perceives the drought signals and maintains its growth and development during drought. Under drought conditions, phenotyping of roots demonstrates the relevance of root characteristics as a screening tool for drought resistance. Phenotyping helps to understand how various root characteristics contribute to drought tolerance by drawing soil resources from deeper soil layers and using them to carry out many metabolic processes in the plant system. Deeper rooted plants can draw water from the soil at a deeper level, which protects them from drought stress (Bao et al. 2014).

Under water stress, root traits are critical for maintaining crop yields because they affect water and nutrient absorption (Narayanan et al. 2014). Plants with a larger main root have more growth potential since it is directly related to water absorption and has a greater ability to penetrate the compacted soil. Particularly, herbaceous plants have thin roots, which are more permeable and better able to absorb water. Due to increased climate variability under current cropping systems, this role is considered even more important in soils with low water and nutrient availability. Root architecture has a substantial influence on nitrogen-usage efficiency. As the roots grow deeper and faster, more adventitious roots are formed in the upper soil layer, which increases nutrient and water uptake and reduces soil surface evaporation losses (Sinclair 1994). The initiation, branching, and turnover of new roots are all regulated by soil temperature. The increase in root characteristics such as root length and volume, during a water shortage and after recovery, is linked to greater drought tolerance. Water may be conserved by increasing partitioning to root mass, which would result in a tendency to allocate less assimilates to other parts of the plant. Rapid root development into the surrounding soil would be an adaptive benefit in using the soil water more completely. Several root traits, such as root tissue density, specific surface area, and specific root length are also linked to higher crop yield under drought. The diameter of the roots and the density of the root tissue determine the surface area and length of the roots, respectively. A bigger root system and deeper rooting ability will support the acquisition of required soil water under stress conditions, where deeper soil water is accessible and contributes to sustaining yield under terminal drought conditions.

### 11.2.2 Reproductive Responses

When drought is induced shortly before the reproductive growth of groundnut, a large burst in flowering may represent a distinctive characteristic in the pattern of flowering under moisture stress. The main flush of flowers generated up to 45 days after planting does not form pegs when stress is imposed (30–45 days after sowing); however, this loss is compensated by the flowers produced after rewatering (Gowda and Hegde 1986). The ultimate groundnut yield is determined by the flowering pattern or the number of flowers produced at various stages of the reproductive cycle. After 75–90 days of post-flowering water stress, groundnut plants act like watered ones and produce more flowers. The flowering time of groundnuts is around 41–60 days; however, plants exposed to water stress during this period have fewer flowers, because the plants have followed a 51–70 days' flowering pattern. Water-stressed plants had more early-formed flowers, which determine the optimum flowering pattern of 31–50 days, even if they had fewer flowers overall than plants that were exposed to stress after flowering (Kalarani et al. 2018). Drought stress slows groundnut peg elongation, which is turgor dependent and delays pod and seed development due to dry soil at the pegging zone. Soil water deficiencies in the pegging and root zone reduced pod and seed development rates by around 30% and lowered the weight per seed by 428–563 mg.

Studies showed that at higher air temperatures, pod yield reduced due to fewer pegs and pods as a result of less fruit set. Ketring (1984) found that exposure to day temperature of 35 °C reduced the number of pegs and pods by 33% when compared to 30 °C under a controlled environment. When flowering and pod development occurred at a temperature of 40 °C, pod yield dropped by more than 50% of its potential yield. Heat stress significantly reduced kernel weight by 45–46% compared to non-stressed environments.

### 11.2.3 Physiological Responses

There is a negative impact of abiotic stress on groundnut, which is plant water relations and mineral nutrition as well as metabolism and photosynthesis (Suthar and Patel 1992). Under abiotic stress conditions, biomass output and pod yield are used as selection standards for resistant groundnut genotypes. Many factors, including relative water content (RWC), leaf water potential (WP), stomatal resistance, transpiration rate, leaf temperature, and canopy temperature, affect the groundnut water relations under drought. Plants that are under stress have lower RWC values than plants that are not under stress. The radiation and vapor pressure deficits are low in the morning, and the groundnut leaves have high RWC values. By midday, low values were observed, and after midday, again gradual increase in RWC values was observed (Erickson and Ketring 1985).

Water-deficit plants lose moisture from pods, which reduces the physiological activity of seeds, and so inevitably both yield and nutritious quality are affected. The characteristics related to drought tolerance and pod production exhibit significant

relationships between drought tolerance index (DTI), pod yield, root length density (RLD), and harvest index (HI), demonstrating that RLD in deeper soil contributes to pod yield and HI under drought circumstances. In the pegging and root zones, a lack of water can reduce pod and seed output by 30% (Kambiranda et al. 2011). As previously reported in groundnut (Sheshshayee et al. 2006; Songsri et al. 2008), a strong direct association between water-usage efficiency (WUE) and chlorophyll index as well as an indirect correlation between leaf area and SPAD chlorophyll meter readings (SCMR) have been found. Maheswari et al. (2016) found that drought had a beneficial effect on plant osmotic adjustment and photosynthetic rate during the pre-flowering period when plants were exposed to drought. Drought stress kills the chlorophyll and inhibits its production in groundnut. A higher chlorophyll a/b ratio with a decreasing total chlorophyll content indicates more damage to chlorophyll b than chlorophyll a (Mafakheri et al. 2010).

Temperature-induced adaptations in plants include long-term evolutionary changes in phenology and molecular structure as well as short-term avoidance or acclimation strategies involving leaf orientation and transpiration cooling. High temperature has detrimental effects on plants, such as lower leaf water potential, reduced leaf area, and premature leaf senescence. These factors all have an impact on the plant's photosynthetic ability (Greer and Weedon 2012). Drought and salt stress are known to be harsher on shoot growth than on root growth. Plants might preserve soil moisture by using less water if their leaf area expansion was reduced in relation to their root growth. Water absorption is restricted in salt-stressed organisms, and this causes osmotic stress. Salt stress also increases the buildup of  $\text{Na}^+$  and  $\text{Cl}^-$  ions, which can cause cytotoxicity, impede enzyme activity, and lead to other elements being unbalanced. Salt stress impairs cellular metabolism and photosynthetic activity.

### 11.2.4 Biochemical and Molecular Responses

When plants are under abiotic stress, their cellular biochemistry is altered such as protein content, ion transporters, signal molecules, free radical scavengers, and other biochemical reactions. The stress caused by drought and high temperatures promotes the formation of reactive oxygen species (ROS), which inactivate enzymes, damage cellular components, and decrease the defense capability of the plants. High temperatures have a significant impact on starch and sucrose synthesis because they lower the activity of enzymes including sucrose phosphate synthase, ADP-glucose pyrophosphorylase, and invertase. Under conditions of sufficient water supply, the transpiration rate is often correlated with the incident radiation. Drought-stressed plants lose more water through transpiration than healthy ones. As well as rendering groundnuts more prone to aflatoxin contamination (Cole et al. 1989), this makes them unsuitable for human consumption.

When membranes are subjected to high temperatures, they experience lipid bilayer stress, which allows membrane proteins to displace and solutes to leak, also leading to deterioration of membrane selectivity (Du et al. 2011). Physiological

characteristics, such as leaf area and chlorophyll concentration, were linked with membrane damage in groundnut under high-temperature stress. Free radical production compromises a plant's defense capabilities, resulting in oxidative stress. Additionally, the Fenton/Haber-Weiss pathway generates a harmful hydroxyl radical ( $\cdot\text{OH}$ ) inside the plants, which destabilizes the membrane lipids through lipid peroxidation, resulting in membrane damage. Damage to cellular membranes and chlorophyll is a good measure of how much oxidative stress has damaged the plant.

There are numerous ways in which plants alter their metabolism in response to abiotic stress, including producing compatible solutes that can organize proteins and cellular structure to keep the cell turgor, as well as making changes to the antioxidant system to restore cell redox balance and maintain homeostasis (Janská et al. 2010). Due to abiotic stress, modification of physiological and biochemical processes by gene expression changes gradually leads to the development of tolerance in the form of acclimation or, in the ideal case, to adaptation (Mirza et al. 2010).

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## 11.3 Tolerance Mechanisms and Adaptation

### 11.3.1 Morphophysiological Mechanisms

Understanding the abiotic stress tolerance mechanism through the physiological and genetic processes of plants helps in the development of the newest varieties with abiotic stress tolerance. Plants have numerous adjustment responses to abiotic stress, including stomatal behavior and osmotic changes. The adaptive response of the plant to survive under long-lasting drought is in relation to decreased oxidative damage to cells (Azevedo Neto et al. 2010). Groundnut crop might undergo closure of stomata during drought in semiarid regions. Prolonged water shortages combined with high temperatures can limit active gas exchange duration gradually by stomatal behavior, which impacts plant growth and development processes. But the quick and complete recovery from severe stress after rewatering leads to normal stomatal conductivity, which is frequently recorded in groundnut. This ability to quickly recover to normal transpiration and  $\text{CO}_2$  assimilation is a key mechanism for the adaptive reactions of the groundnut. Higher palmitic and stearic acid accumulations in groundnut at high temperatures improve membrane stability.

Cellular activities of plants are altered differently when exposed to a particular abiotic stress or when combined with specific stress environments. In addition to these changes, the production and accumulation of highly soluble, low-molecular-weight, electrically neutral, nontoxic compounds, generally known as osmolytes or osmoprotectants (Behelgardy et al. 2012), are important due to their protective role against the damage that was done by the stress, which could affect the cellular machinery. These compounds directly scavenge toxic ROS and protect antioxidant enzymes, thereby improving plants' antioxidant defense system. As a result, osmoprotectants function to activate genes associated with defense mechanism under a various stress. Thus, to survive under hostile conditions, plants have evolved the osmoprotectants as an important evolutionary strategy. Plant cells are protected

against the damaging effects of diverse environmental stresses by amino alkanolic acid proline, which functions as a molecular chaperone.

An increased accumulation of soluble sugars (beta-D-galactofuranoside, hexopyranose, D-glucopyranose) and osmoprotectors (D-mannitol and pentitol) in the groundnut may have played a key role in regulating osmotic changes and in protecting diverse cell structures from temperature stress via maintaining cellular water balance and membrane stability, as well as buffering the cellular redox potential. The increased availability of carbohydrates during heat stress is an essential physiological feature associated with stress tolerance and acclimatization processes.

Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR), and other associated enzymes involved in the cellular detoxification are considered as the primary critical defense mechanism towards abiotic stresses. Drought-induced damage was mitigated with an increase in SOD and POD activities. It is the tolerance capacity, mainly dependent on genotypes. POD and SOD activities are increased with the progression of water stress to a certain degree and subsequently stabilized in certain genotypes and have very little activity in certain genotypes, which are sensitive genotypes (Maheswari et al. 2018). The initial line of defense is SOD, which detoxifies the superoxide radicals into hydrogen peroxide ( $H_2O_2$ ); CAT and POD break down  $H_2O_2$ . The conversion of  $H_2O_2$  to the nontoxic water molecule is via either CAT activity or ascorbate-glutathione cycle. This process limits the cellular buildup of  $H_2O_2$ . Finally, glutathione reductase performs NADPH-dependent reduction of oxidized glutathione (GSSG) to reconstitute the cellular pool of reduced glutathione (GSH) (Noctor et al. 2002).

### 11.3.2 Molecular Mechanisms

The use of diverse methodologies has assisted scientists in drawing a global picture of how plants perceive environmental stress signals, transmit the stress signals to the nucleus, and then regulate gene expression to create appropriate responses when stressed. Although insights into plant tolerance mechanisms, as well as particular activities of various participants and their interactions with other members within the network, have not yet been precisely characterized, several different network components have been targeted and utilized for genetic modification.

Transcription factors (TFs), kinases, phosphatases, microRNAs (miRNAs), and two-component systems (TCSs) have all been discovered as members of genes that encode regulatory proteins that play important roles in influencing plant behavior in response to abiotic stresses (Hoang et al. 2014). The role of regulatory members is to transfer stress signals from the external environment to the nucleus (such as TFs and TCSs) and to directly control the gene expression (like TFs) by interacting with gene promoters. In eukaryotes, small ubiquitin-like modifier (SUMO) peptide binding to protein substrates (SUMOylation) is a key posttranslational regulation mechanism. SUMOylation was shown to play a vital role in pod formation and abiotic stress.

The expressional control of auxin transporters, including ABCB transporters, is crucial in drought response. Plant response to abiotic stress might be improved by engineering hormone signaling. Exogenous brassinolide (BR) increased cucumber photosynthesis through influencing photosynthetic enzymes such as ribulose 1,5 biphosphate carboxylase/oxygenase (Rubisco). To control photosynthesis, BR signaling might move from brassinosteroid insensitive (BRI) to transcription factors brassinazole resistant 1 (BZR) and phytochrome interacting factors (PIFs) (Osakabe et al. 2014). As a result, BR priming may be able to control photosynthesis transcriptionally during drought stress. Exogenous BR signal promotes auxin biosynthesis and expression of the transcription factor genes, such as small auxin upregulated 15 (SAUR15). As a result, the enhanced growth might be due to the cross talk between the BR signal and the auxin signal during BR priming. Plant defense against stress is regulated by salicylic acid (SA), jasmonic acid (JA), and abscisic acid (ABA).

Protein analysis is a straightforward way to determine the function of their linked genes. Proteome analysis linked with genome sequence data is important for functional genomics. However, the data on protein expression that is now accessible is inadequate. Spectroscopy study of changes in seed protein composition in response to drought stress indicated that methionine-rich proteins (MRPs) and arachin proteins were downregulated in drought-susceptible (DS) genotypes, but not in drought-tolerant (DT) genotypes. The upregulation of mRNA transcripts in DT genotypes showed a link to stress tolerance. Continued production of those proteins appears to improve drought tolerance; it lowers the aflatoxin levels and increases the nutritional value of groundnuts (Basha et al. 2007).

Metabolomics is an interdisciplinary branch of study that focuses on the metabolomes of biological systems. Metabolomics, as a high-throughput technology, has the fundamental goal of providing a comprehensive view of all metabolites participating in cellular processes, which necessitate the use of nonselective, universally applicable, and comprehensive analytical approaches for metabolite identification and quantification. Relative electrolyte leakage (REC) fluctuation in reaction to salt stress, particularly during recovery, was demonstrated by metabolite changes, with 92 metabolites, out of a total of 391 detected, varying in response to salt and 42 metabolites responding specifically to recovery. Transcriptomics data revealed that 1742 transcripts in shoots and 3281 transcripts in roots changed in response to salt stress, whereas 372 transcripts in shoots and 1386 transcripts in roots responded particularly to recovery but not salt stress. Finally, 95 transcripts and 1 metabolite were identified as potential candidates for REC, photosynthesis, transpiration, and variation in  $\text{Na}^+$  accumulation (Cui et al. 2018).

Dehydration-responsive element binding (DREB) (a member of the ethylene-responsive element-binding factor (ERF) family) has been shown to efficiently alter the expression of several stress-inducible genes in groundnut, therefore conferring drought tolerance. Groundnut transgenic lines had a higher proline content (30–40%) and higher levels of pyrroline-5-carboxylate synthase (P5CS) than non-transgenic plants during drought and salt stress. Transgenic groundnut plants not only pile up a lot of solutes, but they also had better membrane integrity under



stress. Groundnut transgenics overexpressing AtNAC2 (*Arabidopsis* NAM, ATAF1, 2, and CUC2) demonstrated better drought and salinity tolerance as well as yield under water-stressed circumstances.

Compared to the wild-type plants, transgenic groundnut plants containing a novel stress-inducible WRKY transcription factor, MuWRKY3 (*Macrotyloma uniflorum* Lam. Verdc) gene isolated from horse gram, improved drought tolerance by slowing down the wilting; upregulating stress-inducible genes; accumulating higher proline, total sugars, and antioxidant enzymes; and lowering malondialdehyde, hydrogen peroxide, and superoxide anion. *Arabidopsis* homeodomain-leucine zipper transcription factor (AtHDG11) was overexpressed under stress-inducible promoter desiccation-responsive protein 29A (rd29A), which increased drought and salt tolerance in transgenic groundnut plants by upregulating stress-responsive genes, antioxidative enzymes, and free proline. Furthermore, the transgenic plants had longer roots, lower stomatal density, higher chlorophyll content, greater specific leaf area, and better photosynthetic rates (Banavath et al. 2018). At NAC2, groundnut transgenics showed a lower rate of water loss and higher RWC than wild type, indicating that transgenics had a greater ability to retain water and maintain a higher leaf water status. One of the major factors that result in the preservation of a greater canopy photosynthetic rate during stress is the maintenance of higher chlorophyll content, which indicates the stay-green nature of AtNAC2 transgenics under stress conditions. Transgenics have also shown less membrane damage when stressed. When the PDH45 gene (pea DNA helicase) was overexpressed in genetically modified groundnut, it showed about 10% higher yield under salt stress.

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## 11.4 Strategies for Improving Abiotic Stress Tolerance

Complete groundnut sequencing will be too expensive and labor consuming to undertake with existing resources. The cultivated form of groundnut is an amphidiploid with  $2n = 4x = 40$  chromosomes. The study of molecular features of the groundnut genome began in the 1980s, when protein and isozyme variation in groundnut was shown to be ineffective for defining variation in the cultivated groundnut. Although many polymorphisms were found in other species within the genus, the number of markers was too small to be used in breeding programs on a regular basis.

Gene knockout and knockdown strategies based on ethyl methane sulfonate, T-DNA insertion mutations, transposable element insertion, target-induced local lesions in genomes, and gene silencing by RNAi have been used, but these methods have drawbacks such as the need to screen large populations of mutants and transgenic lines. These issues may be avoided by using virus-induced gene silencing (VIGS), and a strong functional genomics method will be employed to create multi-stress-resistant groundnut plants. However, the creation of VIGS procedures to examine the activity of a single gene under many stressful situations in a given time frame is required.

Seed priming has the potential to enhance seed germination, produce anti-stress chemicals, and acclimatize groundnut to abiotic stresses. Breeding for abiotic stress resistance has been a critical technique used by researchers to relieve abiotic stress issues and ensure to meet out the abiotic stress-prone environments (Pereira et al. 2012). Understanding physiology and genetics may lead to a better understanding of stress response and assist in the creation of new stress-tolerant cultivars. However, due to the number and order of genes regulating quantitative characteristics, the transmission of features associated with abiotic stress adaptation is likely to be genetically complicated.

Although there is significant phenotypic diversity for yield-related characteristics in groundnut, the variability for vitamin (primarily vitamin E) and micronutrient (particularly Fe and Zn) levels, as well as resistance to aflatoxin, insect, and disease, is extremely low in the cultivated groundnut. Because of the minimal diversity of the abovementioned characteristics, genetic improvement of groundnut by traditional and marker-assisted breeding is limited.

Stress-inducible expression of AtHDG11 in three independent homozygous transgenic groundnut lines improved the drought and salt tolerance by upregulating known stress-responsive genes (LEA, HSP70, Cu/Zn SOD, APX, P5CS, NCED1, RRS5, ERF1, NAC4, MIPS, aquaporin, TIP, ELIP) in the stress gene network, antioxidative enzymes, and free proline and enhanced water-use efficiency traits such as longer root system, reduced stomatal density, higher chlorophyll content, increased specific leaf area, improved photosynthetic rates, and increased intrinsic and instantaneous WUE. Transgenic groundnut plants outperformed non-transgenic plants in terms of yield under both drought- and salt-stress conditions. Transgenic methods would aid in the introduction of those genes into groundnut to improve mineral content, vitamin E content, and aflatoxin resistance.

Direct irradiation of groundnut seed or seeds of mutant(s) produced from it will result in a modified salt tolerance level. The clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9 (CRISPR–Cas9) system has great potential for evaluating gene/genome function and developing abiotic stress tolerance in a variety of plants. It is a low-cost, simple, user-friendly, and fast-accepted genome editing technology for generating genome-edited crops to meet rising food demands in the face of climate change. To better understand the underlying metabolism, it is critical to identify and classify the individual genes linked with the complicated processes of tolerance. Plant tissue culture system is an efficient and dependable approach for studying salt tolerance in groundnut. The method is simple to operate, allowing the tolerance potential of the plants to be accurately measured.

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## 11.5 Conclusion

So far, detailed investigations have substantially contributed to a better knowledge of groundnut plant responses in terms of morphophysiological, biochemical, and molecular features under drought, high-temperature, and, to a lesser extent, salt

stress. Several researchers have reported on the underlying adaptation and tolerance mechanisms in groundnut against abiotic stresses such as drought, salt, and high temperature. In addition, numerous drought tolerance techniques have been identified. However, in addition to drought and high-temperature stresses, an in-depth study of groundnut responses to different abiotic stresses such as waterlogging, salt and sodic conditions, low temperature, and low light intensity is required, under changing climatic circumstances. Furthermore, the adaptive characteristics and tolerance mechanisms against each of these stresses must be elucidated in order to be used in breeding programs to create tolerant genotypes. Proteomics, metabolomics, marker-assisted selection, gene editing methods, and transgenic technologies must be used successfully to produce novel groundnut genotypes tolerant to diverse abiotic stresses to preserve agricultural community output and livelihood security.

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## References

- Azevedo Neto AD, Nogueira RJMC, Melo Filho PA, Santos RC (2010) Physiological and biochemical responses of peanut genotypes to water deficit. *J Plant Interact* 5(1):1–10
- Banavath JN, Chakradhar T, Pandit V, Konduru S, Guduru KK, Akila CS, Podha S, Puli COR (2018) Stress inducible overexpression of AtHDG11 leads to improved drought and salt stress tolerance in peanut (*Arachis hypogaea* L.). *Front Chem* 6:34
- Bao Y, Aggarwal P, Robbins NE, Sturrock CJ, Thompson MC, Tan HQ, Tham C, Duan L, Rodriguez PL, Vernoux T (2014) Plant roots use a patterning mechanism to position lateral root branches toward available water. *Proc Natl Acad Sci* 111(25):9319–9324
- Basha SM, Katam R, Naik KSS (2007) Differential response of peanut genotypes to water stress. *Peanut Sci* 34(2):96–104
- Behelgardy MF, Motamed N, Jazii FR (2012) Expression of the P5CS gene in transgenic versus nontransgenic olive (*Olea europaea*) under salinity stress. *World Appl Sci J* 18(4):580–583
- Cole RJ, Sanders TH, Dorner JW, Blankenship PD (1989) Environmental conditions required to induce preharvest aflatoxin contamination of groundnuts: summary of six years' research. In: International workshop on aflatoxin contamination of groundnut, Patancheru, AP (India), 6–9 Oct 1987
- Cui F, Sui N, Duan G, Liu Y, Han Y, Liu S, Wan S, Li G (2018) Identification of metabolites and transcripts involved in salt stress and recovery in peanut. *Front Plant Sci* 9:217
- Du H, Wang Z, Yu W, Liu Y, Huang B (2011) Differential metabolic responses of perennial grass *Cynodon transvaalensis* × *Cynodon dactylon* (C4) and *Poa Pratensis* (C3) to heat stress. *Physiol Plant* 141(3):251–264
- Erickson PI, Ketring DL (1985) Evaluation of peanut genotypes for resistance to water stress in situ I. *Crop Sci* 25(5):870–876
- Gowda A, Hegde BR (1986) Moisture stress and hormonal influence on the flowering behavior and yield of groundnut. *Plant Physiol* 66:835–837
- Greer DH, Weedon MM (2012) Modelling photosynthetic responses to temperature of grapevine (*Vitis vinifera* cv. Semillon) leaves on vines grown in a hot climate. *Plant Cell Environ* 35(6):1050–1064
- Groundnut Outlook (2018) Groundnut Outlook, PJTSAU. pp 1–3
- Hamidou F, Halilou O, Vadez V (2013) Assessment of groundnut under combined heat and drought stress. *J Agron Crop Sci* 199(1):1–11

- Hoang XLT, Thu NBA, Thao NP, Tran LSP (2014) Transcription factors in abiotic stress responses: their potentials in crop improvement. In: Improvement of crops in the era of climatic changes. Springer, New York, NY, pp 337–366
- Hoegh-Guldberg O, Jacob D, Bindi M, Brown S, Camilloni I, Diedhiou A et al (2018) Impacts of 1.5 C global warming on natural and human systems. Global warming of 1.5 C. An IPCC special report
- Janská A, Maršík P, Zelenková S, Ovesná J (2010) Cold stress and acclimation—what is important for metabolic adjustment? *Plant Biol* 12(3):395–405
- Kalarani MK, Maheswari P, Senthil A, Umapathi M (2018) Influence of pre flowering drought on physiological parameters and yield in groundnut. *Madras Agric J* 105:378–380
- Kambiranda DM, Vasanthaiah HKN, Katam R, Ananga A, Basha SM, Naik K (2011) Impact of drought stress on peanut (*Arachis hypogaea* L.) productivity and food safety. *Plants Environ*:249–272
- Ketring DL (1984) Temperature effects on vegetative and reproductive development of peanut. *Crop Sci* 24(5):877–882
- Mafakheri A, Siosemardeh AF, Bahramnejad B, Struik PC, Sohrabi Y (2010) Effect of drought stress on yield, proline and chlorophyll contents in three chickpea cultivars. *Aust J Crop Sci* 4(8):580–585
- Maheswari P, Kalarani MK, Senthil A, Sowmiyapriya S (2016) Physiological and yield responses of groundnut (*Arachis hypogaea* L.) genotypes to drought. *Madras Agric J* 103:309–313
- Maheswari P, Kalarani MK, Senthil A, Umapathi M (2018) Effect of pre flowering drought on flowering behaviour of yield in groundnut. *Madras Agric J* 105:368–369
- Mirza H, Hossain MA, Fujita M (2010) Physiological and biochemical mechanisms of nitric oxide induced abiotic stress tolerance in plants. *Am J Plant Physiol* 5(6):295–324
- Narayanan S, Mohan A, Gill KS, Prasad PVV (2014) Variability of root traits in spring wheat germplasm. *PLoS One* 9(6):e100317
- Noctor G, Veljovic-Jovanovic S, Driscoll S, Novitskaya L, Foyer CH (2002) Drought and oxidative load in the leaves of C3 plants: a predominant role for photorespiration? *Ann Bot* 89(7):841–850
- Osakabe Y, Osakabe K, Shinozaki K, Tran L-SP (2014) Response of plants to water stress. *Front Plant Sci* 5:86
- Pereira J, MeloFilho P, Albuquerque M (2012) Mudanças bioquímicas em genótipos de amendoim submetidos a déficit hídrico moderado. *Rev Cienc Agron* 43:766–773
- Prasad PVV, Craufurd PQ, Summerfield RJ (1999) Fruit number in relation to pollen production and viability in groundnut exposed to short episodes of heat stress. *Ann Bot* 84(3):381–386
- Reddy TY, Reddy VR, Anbumozhi V (2003) Physiological responses of groundnut (*Arachis hypogaea* L.) to drought stress and its amelioration: a critical review. *Plant Growth Regul* 41(1):75–88
- Sheshayee MS, Bindumadhava H, Rachaputi NR, Prasad TG, Udayakumar M, Wright GC, Nigam SN (2006) Leaf chlorophyll concentration relates to transpiration efficiency in peanut. *Ann Appl Biol* 148(1):7–15
- Sinclair TR (1994) Limits to crop yield? In: Physiology and determination of crop yield, pp 509–532
- Songsri P, Jogloy S, Vorasoot N, Akkasaeng C, Patanothai A, Holbrook CC (2008) Root distribution of drought-resistant peanut genotypes in response to drought. *J Agron Crop Sci* 194(2): 92–103
- Suthar DM, Patel MS (1992) Yield and nutrient absorption by groundnut and iron availability in soil as influenced by lime and soil water. *J Indian Soc Soil Sci* 40(3):594–596
- Zafar SA, Noor MA, Waqas MA, Wang X, Shaheen T, Raza M, Rahman MU (2018) Temperature extremes in cotton production and mitigation strategies. Past, present and future trends in cotton breeding. *IntechOpen*, London, pp 65–91