Chapter 10
Effects of Drought Stress on Agricultural Plants, and Molecular Strategies for Drought Tolerant Crop Development

Shashi Ranjan, Aman Prakash, Raj Bahadur Singh, Pragalbh Tiwari, Sayan Bhattacharya, Potshangbam Nongdam, Abdel Rahman Al-Tawaha, Milan Kumar Lal, Rahul Kumar Tiwari, Sayanti Mandal, and Abhijit Dey

Abstract In natural environment, plants are subjected to encounter various kinds of abiotic stresses. Drought stress is the inevitable factor that onsets without the identification of any borders or without any warning. It is the most significant environmental stress brought on by fluctuations in temperature, light intensity, and low rainfall. It deteriorates plant biomass production, quality, and energy, leading to adverse effects

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S. Ranjan · A. Prakash
Department of Molecular and Cellular Engineering, Jacob Institute of Biotechnology and Bioengineering, Sam Higginbottom University of Agriculture, Technology and Sciences (SHUATS), Prayagraj, Uttar Pradesh 211007, India

R. B. Singh
Department of Botany, Institute of Science, Banaras Hindu University, Lanka, Varanasi 221005, India

P. Tiwari
College of Forestry, Sam Higginbottom University of Agriculture, Technology and Sciences (SHUATS), Prayagraj, Uttar Pradesh 211007, India

S. Bhattacharya
School of Ecology and Environment Studies, Nalanda University, Rajgir, Nalanda, Bihar 803116, India

P. Nongdam
Department of Biotechnology, Manipur University, Canchipur, Imphal, Manipur 795003, India

A. R. Al-Tawaha
Department of Biological Sciences, Al-Hussein Bin Talal University, Maan, Jordan

M. Lal · R. K. Tiwari
ICAR-Central Potato Research Institute, Shimla, Himachal Pradesh 171001, India

S. Mandal (✉)
Department of Biotechnology, Dr. D. Y. Patil Arts, Commerce & Science College, Sant Tukaram Nagar, Pimpri, Pune, Maharashtra 411018, India
e-mail: mandalsayanti@gmail.com

Institute of Bioinformatics and Biotechnology, Savitribai Phule Pune University, Ganeshkhind Road, Pune, Maharashtra 411007, India

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on the growth and production of plants. Abiotic stress causes physical damage, physiological and biochemical disruptions, and molecular changes. Depending on the species, plants have developed a variety of intricate resistance and adaptive mechanisms, including physiological and biochemical responses, to deal with this stress. Plants have acquired a variety of strategies to deal with drought stress, including altered stomatal conductance and distribution, altered growth pattern and structural dynamics, reduced transpiration loss, increased root length, accumulation of compatible solutes, increased transpiration efficiency, osmotic and hormonal regulation, and delayed senescence. Breeding strategies, molecular and genomics perspectives, emphasizing the alteration of omics technology metabolomics, proteomics, genomics, transcriptomics, genomics, and phenomics that improve plant stress tolerance, and marker-assisted selections are the major drought stress alleviation measures. Additionally, CRISPR-Cas method has opened up new dimensions and promises in developing drought tolerant plants. In the present chapter, the evidence on plant responses to drought stresses are explained and their possible defense measures are discussed.

Keywords Drought stress · Phytohormone · Drought tolerance · Mitigation · Genetic improvement · Molecular breeding

10.1 Introduction

During the growth and development phase, plants inevitably face several stresses which may be due to agricultural and natural conditions. Among all the stresses the plants face, drought is one of the most severe environmental stresses affecting the plants' productivity and growth. The plant body mass comprises about 80–95% of water which plays an important role in several physiological processes (Abbasi and Abbasi 2010; Brodersen et al. 2019). Due to the rapid growth in population and increasing demand for food, drought stress has become problematic in the field of agriculture (O'Connell 2017). Drought condition is very unpredictable, it depends on various factors such as water holding capacity around the rhizosphere, uneven distribution of rainfall, and evapotranspiration, while in some cases it has been found that plants are not able to uptake water from the soil, even there is enough moisture present near the root zone (Seleiman et al. 2021). Such a phenomenon is called physiological or pseudo-drought (Salehi-Lisar and Bakhshayeshan-Agdam 2020). When plants face such evolving conditions, it becomes necessary to enhance the ability of plants to withstand drought. In order to improve water-use efficiency, mere physical adaptations of roots and leaves may prove insufficient. This is where

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A. Dey (✉)
Department of Life Sciences, Presidency University, 86/1 College Street, Kolkata, West Bengal 700073, India
e-mail: abhijit.dbs@presiuniv.ac.in

molecular signals come into play, particularly a specific gene encoding regulatory proteins that govern the expression of numerous other genes. These molecular signals engage in crosstalk through various regulatory mechanisms, enabling the plant to respond effectively to drought conditions (Shahid et al. 2020; Yadav et al. 2020). Here, the fundamental reactions of agricultural plants to drought stress are addressed, as well as the management strategies are discussed which can be followed in order to reduce the negative consequences of this abiotic stress.

10.2 Environmental Factors Responsible for Drought Stress in Plants

The ongoing increase in air temperature and atmospheric CO_2 levels is anticipated to intensify global climate change, leading to significant alterations in rainfall patterns and distribution (Yang et al. 2019; Yin et al. 2018). While insufficient rainfall is typically the primary factor contributing to drought stress, the situation can be exacerbated by the evaporation of water from soils. This evaporation is primarily influenced by high temperatures, intense light, and dry winds, and it can intensify an ongoing drought event (Cohen et al. 2021). The effects of global climate change often led to widespread drought stress across large regions on a global level. In addition to drought, salinity stress is also recognized as a major factor contributing to water deficits in plants (Adnan et al. 2020; Mostofa et al. 2018; Tariq et al. 2020). There are several factors that are responsible for drought stress in plants.

10.2.1 Global Warming

Certain consequences arising from climate change may have positive impacts on agricultural productivity. One such example is the potential increase in photosynthesis rates observed under elevated CO_2 levels. Consequently, the higher concentrations of CO_2 in the atmosphere could potentially enhance grain yields in the future (Brown et al. 2018). Usually, climate change brings about adverse consequences for both natural and agricultural ecosystems. Rising air temperatures can lead to the melting of glaciers, which in turn poses a risk of flooding agricultural lands, particularly those with low or negligible slopes (Cook et al. 2014). Furthermore, the diminishing glaciers are resulting in the reduction of water reservoirs, thereby restricting the availability of water for crops. This trend is progressively worsening over time. In fact, numerous rain-fed agricultural regions worldwide have been experiencing reduction in annual accumulated precipitation because of global warming (Sultan et al. 2019). The impact of global warming extends beyond water loss in the soil, affecting water loss at the plant level as well. Increased temperatures resulting from global warming led to significant transpiration of internal water within plants, intensifying the pre-existing water deficit challenges in diverse agricultural systems worldwide. If the anticipated rise in air temperature reaches approximately 2 degrees Celsius above present levels by the end of this century, an estimated one-fifth of the global population will face severe water deficits, highlighting the extensive impact of such conditions (Ray et al. 2019).

10.2.2 Irregular Rainfall

Areas reliant solely on rainfall for crop production are anticipated to face greater stress compared to regions that have access to irrigation systems such as canals and rivers. In rain-fed areas, drought episodes are closely linked to the distribution of rainfall throughout the year, leading to heightened risks of water stress occurring periodically over specific timeframes (Konapala et al. 2020). The prominent human activities of industrialization, deforestation, and urbanization have significant impacts on rainfall patterns, thereby influencing the availability of water to plants. These activities play a role in climate change, ultimately affecting the overall water availability for plant growth and development (Fatima et al. 2020). During the summer season, various factors contribute to the exacerbation of drought stress on plant growth and development. These include increased atmospheric water demand by plants, higher rates of evaporation and transpiration, and reduced availability of rainfall. The distribution and intensity of rainfall within and across years significantly influence both the management of water resources for plants and the occurrence of drought stress in most scenarios (Karandish and Šimůnek 2017; Seleiman et al. 2021).

10.2.3 Change in Monsoon Patterns

In numerous regions across the world, the monsoon system serves as a crucial source of rainfall, particularly during the summer season. The occurrence of the monsoon is closely tied to temperature, as it acts as the primary driving force behind its formation and dynamics (Ali and Anjum 2016). If current conditions persist, it is anticipated that rain-fed areas will experience a substantial decline of approximately 70% in summer precipitation levels by the beginning of the twenty-second century (Yu et al. 2013). Estimations suggest that the linear rise in atmospheric CO_2 concentration will contribute to increased rainfall, posing adverse effects on crop production. This rise in rainfall levels is anticipated to result in widespread flooding and significant economic losses within the agriculture sector of densely populated countries (Guo et al. 2015; Reddy 2015). In such scenarios, the variability in monsoon rainfall plays a crucial role and will continue to influence the moisture levels of the rhizosphere. This, in turn, significantly impacts plant productivity in specific regions of the world, primarily through changes in the intensity, occurrence, and duration of rainfall. Notably, the shifts in monsoon patterns have led to extreme variations between dry and wet seasonal rainfalls, resulting in significant food insecurity for approximately two-thirds of the global population (Prakash et al. 2020). In addition to the inherently random and unpredictable nature of rainfall patterns, recent climate changes have further contributed to the potential shortening or lengthening of the rainy season. This variability can exacerbate existing and future scenarios, leading to challenges of both water deficit and water excess in certain climatic zones. Given the agricultural context, it is imperative to adapt crop production practices to align with the behavior of the monsoon season and transition towards sustainable crop production methods. Implementing proper management techniques and effective crop planning are two key strategies to address the quantitative shifts experienced during monsoon patterns, whether they involve water deficiency or excessive rainfall (Seleiman et al. 2021).

10.3 Impact of Drought Stress on Plants

Plants that are under drought stress may experience severe effects on their growth, development, and overall health. The plant undergoes changes such as reduction in turgor pressure, closure of stomata during the day, disruption of water potential gradients, change in membrane integrity, leaf rolling, and a decrease in cell development and growth, which are vital for maintaining life processes (Zargar et al. 2017). The drought stress affecting the plant is briefly mentioned and is shown in Fig. 10.1: water deficiency, reduced photosynthesis, stomatal closure, oxidative stress, nutrient imbalance, reduced growth and development, increased susceptibility to diseases and pests, stem extension, and root proliferation (Fig. 10.1).

10.3.1 Water Deficiency

Water scarcity is a major environmental barrier to plant growth and development. The most obvious effect of drought stress is the limited availability of water in the soil. Water is necessary for several physiological functions of plants, such as photosynthesis, nitrogen intake, and transpiration. Drought stress leads to water deficit in plant tissues, disrupting these essential processes. Water scarcity outbreaks are due to the occurrence of less or the absence of rainfall resulting in low soil moisture content and low water potential in aerial parts of the plant such as leaves and stems (Ristvey et al. 2019). In arid environments, the rate at which water is lost by transpiration from leaves outpaces the rate at which water is absorbed by roots. Seed germination is one of the most important phases in the life cycle of a plant, and is highly responsive to its existing surrounding environment (Bahrami et al. 2012). For the success or failure of plant establishment in soil, the prime requirement for germination is the presence of water (Hasanuzzaman et al. 2013).

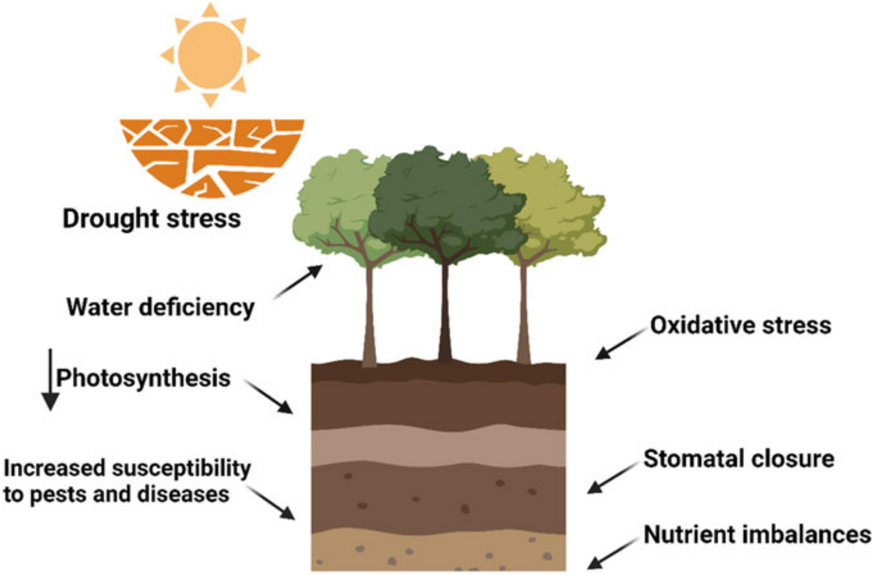

Fig. 10.1 Impact of Drought stress on plants. Image created with BioRender.com (https://biorender.com/)

10.3.2 Reduced Photosynthesis

Photosynthesis is one of the main processes affected by water stress. Leaf photosynthetic products are the material basis of plant growth. (Yang et al. 2021). Drought stress negatively affects photosynthesis, the process by which plants convert light energy into chemical energy. Insufficient water reduces the availability of CO_2, leading to decreased photosynthetic rates. By lowering both leaf area and photosynthetic rate per unit leaf area, drought stress is known to limit photosynthesis. Continued photosynthetic light reactions during drought stress under limited intercellular CO_2 concentration result in the accumulation of reduced photosynthetic electron transport components, which can potentially reduce molecular oxygen, resulting in the production of reactive oxygen species (Basu et al. 2016).

10.3.3 Stomatal Closure

Plants close their stomatal aperture as the first response at the onset of drought to maintain the leaf water potential (Laxa et al. 2019). To conserve water during drought, plants often close their stomata (small openings on the leaf surface that regulate gas exchange). Stomatal closure or metabolic impairment is the major cause of a decreased photosynthetic rate (Basu et al. 2016). Stomatal closure reduces the uptake of carbon dioxide (CO_2) required for photosynthesis and limits the release of oxygen (O_2). Stomatal closure limits leaf absorption of CO_2 and prevents transpiration water loss due to turgor pressure and/or reduced water potential (Yang et al. 2021). This can significantly impair a plant's ability to produce energy and growth. This results in reduced plant productivity, stunted growth, and decreased crop yields.

10.3.4 Oxidative Stress

Most abiotic stressors lead to an increase in ROS production. Reactive oxygen species (ROS) are frequently produced by various plant species growing under different conditions under drought stress (Hasanuzzaman et al. 2012; Hasanuzzaman et al. 2013). During normal circumstances, plants synthesize reactive oxygen species (ROS) as the by-product of different vital physiological phenomena such as photosynthesis and photorespiration (Corpas et al. 2020). These reactive species involved in cellular regulation, act as secondary messengers and as a signaling molecule for different metabolic pathways, including seed germination, senescence, plant growth and development (Gonzalez-Gordo et al. 2020) The production of dangerous ROS like O_2^{*-}, H_2O_2, $^1O_2$, and OH^* beyond the plant's scavenging capacity and causing oxidative stress (Li et al. 2010). According to many researches, chloroplast photochemistry alterations result in an excessive synthesis of highly reactive ROS species (Hasanuzzaman et al. 2020). These detrimental ROSs that are produced cause damage to the cell's proteins, lipids, carbohydrates, and nucleic acids as well as alter cellular homeostasis, which can sometimes result in cell death. So, oxidative stress leads to disrupting normal cellular functioning, impairing plant growth and development.

10.3.5 Nutrient Imbalances

A nutritional imbalance can have an impact on several biological processes. Mineral nutrients help to synthesize vital organic molecules like amino acids and proteins in plants. Mineral uptake by plants is a very effective process due to the large surface area of the roots and their ability to absorb inorganic ions at low concentrations in the soil solution (da Silva et al. 2011). Drought stress affects nutrient uptake by plants. Water deficit situations usually reduce the overall soil nutrient accessibility, root nutrient translocation and ultimately lessen the ion contents in various plant tissues (Kheradmand et al. 2014). The decline in the K was attributable to reduced K mobility, declined transpiration rate, and weakened action of root membrane transporters (Hu and Schmidhalter 2005; Hu et al. 2013.) The stomatal guard cells experience an ionic imbalance between K+ , Cl, and H+ due to drought. This ionic imbalance dominates the turgor pressure in the guard cells, which subsequently controls the closing of the stomata. The strict regulation of stomatal conductance under water deficiency enables plants to minimize water loss through evaporation or transpiration

(Mukarram et al. 2021). Nutrient imbalances can result in nutrient deficiencies or toxicities, thus further affecting plant health and productivity.

10.3.6 Reduced Growth and Development

Cell growth is considered one of the most drought-sensitive physiological processes due to the reduction in turgor pressure (Anjum et al. 2011). Meristematic cell divisions produce daughter cells, and the resulting tremendous proliferation of the new cells is what leads to growth. Under severe water deficiency, cell elongation of higher plants can be inhibited by interruption of water flow from the xylem to the surrounding elongating cells. Drought stress causes impaired mitosis; inhibits cell expansion and division, leading to reduced plant growth (Taiz and Zeiger 2010). It affects the development of leaves, stems, and roots, resulting in smaller plant size, decreased biomass, and shorter root systems. In addition to reducing the production of flowers and fruits, drought stress can also result in early leaf senescence (yellowing and shedding).

10.3.7 Increased Susceptibility to Pests and Diseases

Plants are drought susceptible to secondary stresses including pests and pathogens. The impacts of these factors may lead to acute or chronic responses and hosts may respond in different ways in terms of time and space depending on the timing and strength of the stress. There are complex processes involved in tree performance and mortality, and often it can be difficult to identify the leading cause of growth decline and death (Whyte et al. 2016). Plants are less able to tolerate and recover from pest infestations and disease attacks because their defensive systems have been impaired, as well as their physiological processes.

10.4 Plant Response to Drought Stress

Plants in their natural environments respond to environmental drought stress in several ways, from temporary reactions to low soil moisture to significant survival strategies, such as early blooming in the absence of seasonal rainfall. The chart given below provides a brief about the responses involved in drought stress and the factors present in the plants which show response to the stress.

Plants exhibit a range of physiological, biochemical, morphological, and molecular level responses to drought stress are observed in plants. These responses collectively enable plants to survive and adapt to drought stress. By conserving water, adjusting their metabolism, and protecting cellular components, plants increase their

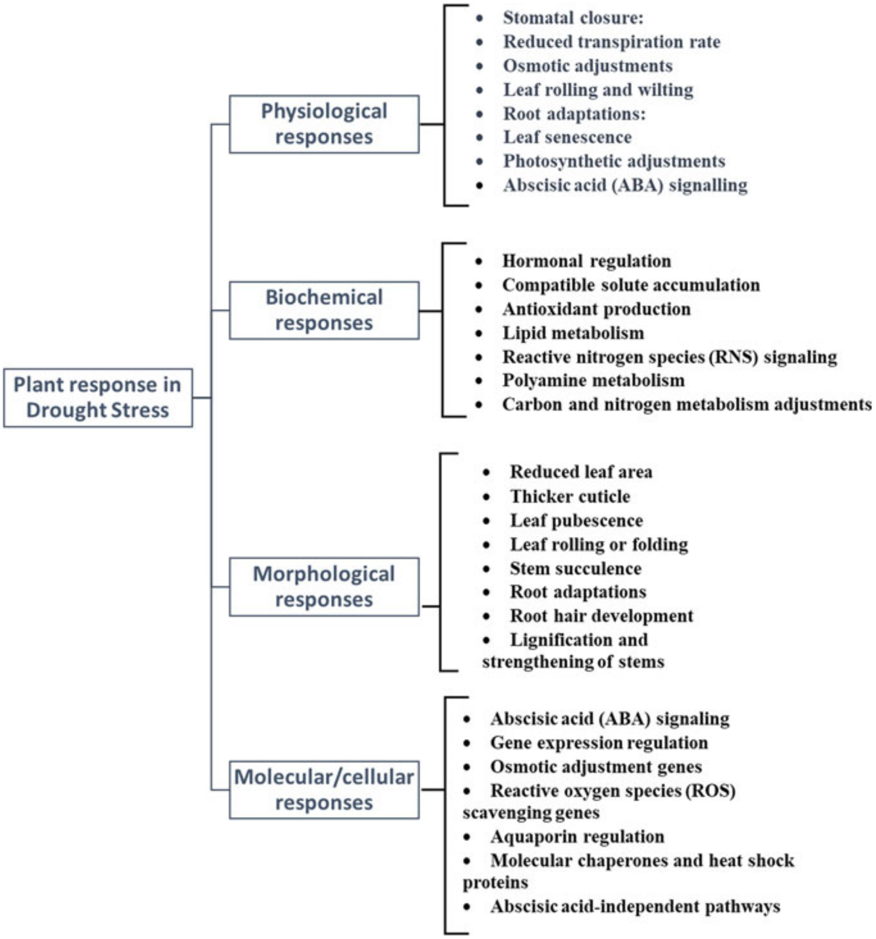

Fig. 10.2 Plant response to drought stress

chances of enduring water-limited conditions and resuming growth and development when water availability improves (Fig. 10.2).

10.4.1 Stomatal Regulation

The closing of stomata is one of the main reactions of plants to drought stress. In addition to allowing for the exchange of gases such as carbon dioxide and oxygen, stomata on the surface of leaves also permit the release of water vapor through transpiration. Plants have a complex signaling system to regulate stomatal opening mediated by the uptake and intracellular synthesis of solutes that reduces the water potential in guard cells and creates a driving force for water uptake (Zhao et al. 2018). To reduce the effects of the drought and prevent excessive transpiration water loss, the stomatal aperture must be dynamically regulated. Stomatal behavior plays a critical role during drought sensing and signaling, yet its modus operandi and crosstalk with other plant phenomena are complex and debatable (Golldack et al. 2014; Lawson and Matthews 2020). During drought, plants close their stomata to reduce water loss. This closure is mediated by hormonal signals, such as abscisic acid (ABA), which is produced in response to water stress.

10.4.2 Leaf Modifications

Plants experiencing drought stress often reduce their leaf area to minimize water loss through transpiration. This can occur through leaf abscission, where older leaves are shed, or through a decrease in leaf expansion and growth. By reducing the overall leaf surface area, plants can conserve water and maintain water balance more effectively. Plants may exhibit various leaf modifications to cope with drought stress. Some plants respond to drought stress by developing leaf pubescence, which is the presence of fine hairs or trichomes on the leaf surface. Trichomes create a layer of boundary air that reduces air movement and thus decreases transpiration rates. They also reflect sunlight, reducing leaf temperature and water loss through evaporation. To reduce water loss through transpiration, plants may exhibit leaf rolling or folding. This morphological response reduces the exposed leaf surface area and creates a protective microenvironment that reduces water loss. Leaf rolling can be observed in grasses, while leaf folding is seen in plants like legumes. Some plants have thick cuticles, which are waxy layers on the leaf surface that reduce water loss through transpiration. Others have smaller or fewer leaves, which helps to decrease the overall surface area for transpiration. In extreme cases, plants may shed their leaves entirely (deciduous plants) to conserve water.

10.4.3 Root Adaptations

The root system detects drought stress first. Even though under these circumstances shoot development is impeded, it continues to grow beneath the earth. Although the growth of the primary root is not affected by drought stress, the growth of lateral roots is significantly reduced, mainly by suppression of the activation of the lateral root meristems (Hasanuzzaman et al. 2013). Plants respond to drought stress by altering their root growth and architecture. They might extend their current roots or create deeper, taproot-like structures to delve deeper into the earth in quest of water. This makes it possible for plants to utilize water supplies that are not present close to the soil surface. Additionally, plants may increase the density of root hairs, which are small outgrowths on the root surface that enhance water absorption.

10.4.4 Antioxidant Production

Drought stress often leads to the generation of reactive oxygen species (ROS), which can cause oxidative damage to plant cells. The well-known antioxidant enzymes in plants include glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), glutathione-S-transferase (GST), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), glutathione-*S*-transferase (GST), and so on (Gill and Tuteja 2010). These are divided into enzymatic and non-enzymatic defense systems that function together to control the flow of uncontrolled oxidation under various stress conditions and protect plant cells from oxidative damage by scavenging ROS (Hasanuzzaman et al. 2013). Production of these antioxidants in plants, scavenge ROS and protect cells from oxidative stress.

10.4.5 Osmotic Adjustments (OA)

Osmotic adjustment is a mechanism to maintain water relations under osmotic stress. Drought stress can cause cellular dehydration due to water loss. OA has been linked to sustaining stomatal conductance, photosynthesis, leaf water volume, and growth during drought stress. In response, plants may accumulate osmolytes, such as sugars, amino acids, and proline, which help maintain cellular hydration and protect proteins and membranes (Farooq et al. 2009). These osmolytes increase the osmotic potential of cells, allowing them to retain water and prevent damage.

10.4.6 Hormonal Regulations

Plant hormones play a crucial role in regulating plant responses to drought stress. Major phytohormones, such as abscisic acid (ABA), cytokinin (CK), gibberellic acid (GA), auxin, and ethylene, regulate diverse processes which enable plant adaptation to drought stress (Wilkinson et al. 2012). These hormones regulate a range of physiological and biochemical changes in plants, including stomatal closure, root development, and the activation of genes that respond to stress. The net outcome of the drought stress response is regulated by a balance between hormones that promote and those that inhibit the trait, rather than the individual action of the hormones (Basu et al. 2016).

10.5 Molecular Methods to Mitigate the Adverse Effect of Drought Stress

Drought stress is an inescapable factor that crosses boundaries and has a negative impact on plant growth, quality, and energy production. It is a substantial environmental stress induced by temperature fluctuations, light intensity, and a lack of rainfall. It is a complicated process that drastically modifies many aspects of plants, including their physical structure, functioning, chemical composition, and molecular features, resulting in a reduction in their ability to perform photosynthesis. Vegetation has developed complicated strategies to withstand and adjust to water deprivation, requiring species-specific anatomical and biochemical reactions (Seleiman et al. 2021).

Researchers are particularly interested in using microbes, hydrogels, nanoparticles, and metabolic engineering techniques to improve plants' drought tolerance. These measures include techniques such as controlling antioxidant enzyme activity, maintaining cellular homeostasis, and minimizing the negative effects of water stress. The goal is to increase plant resilience to drought conditions and lessen the negative effects of water scarcity (Seleiman et al. 2021).

By implementing optimal management practices for planting timing, plant density, plant types, and soil and nutrient management, yield losses in field crops exposed to drought stress can be effectively reduced (Parry et al. 2005; Adeyemi et al. 2020). However, as a notable technique for relieving drought stress, the use of genetically engineered plants possessing drought-tolerant characteristics has attracted substantial attention. Drought-tolerant plants are being developed using a variety of methodologies, including classic breeding techniques, and molecular and genomic approaches (Oliveira et al. 2020), where efforts are primarily focused on boosting water extraction efficiency, water consumption efficiency, stomatal conductance, osmotic adjustments, and other features with the objective of improving the plant's ability to endure drought conditions (Naeem et al. 2020). Other techniques include the use of contemporary and more efficient irrigation technologies, proper planting practices, mulching, contouring, the use of osmoprotectants, and the inoculation of plants with specific microbes proven to improve drought tolerance (Solis et al. 2018*)*.

10.5.1 Selection and Breeding Strategies

Until now, traditional breeding procedures have depended on empirical selection based on yield (Galaitsi et al. 2016). The quantitative trait of yield in key staple crops is predominantly impacted by low heritability and considerable genotype-environment interaction (Scopel et al. 2013). As a result, conventional breeding practices are currently being used to increase production (Aslam et al. 2015). Understanding plant physiological processes is required for identifying quantitative trait loci, locating gene sequences, and breeding in quantitative trait loci (Medici et al. 2014). Due to the irregular, unstable, and unpredictable character of drought response, screening for resistant cultivars under open conditions is not practical. However, such screening can be carried out in shielded and/or regulated situations (Ali et al. 2017).

Classical breeding, on the other hand, refers to the effective method of evaluating randomly selected progenies for better drought resistance across varied habitats (Araujo et al. 2015). Under normal conditions, cultivars with low transpiration rates and unchanged water use efficiency (WUE) have little effect on the final yield (Tejero et al. 2018). As part of their examination, researchers are currently conducting genetic analyses of root architecture, relative water content, and osmotic potential (Bertolino et al. 2019). It is critical to prioritize yield-contributing traits with high heredity that affect grain output under drought conditions, even if they do not have the same effect under ideal conditions. This prioritization is based on the ease with which these attributes may be measured (Shavrukov et al. 2017). However, in agricultural systems with restricted water supply, these variables exhibit broad-sense heritability for yield and frequently do not interact with grain production (Curin et al. 2020). In cases of drought stress, the first and most important element that emerges is a decrease in water use efficiency (WUE), which might vary between types and cultivars (Vishwakarma et al. 2017). In such cases, plants respond by reducing the number of stomata and the size of their leaves, which aids in minimizing water loss and maintaining internal water balance (Ding et al. 2021). As a result, certain genotypes and cultivars are susceptible to drought and are unable to adjust to environmental conditions, resulting in low Water Use Efficiency (WUE) (Tardieu et al. 2018). As a result, using a breeding strategy can help to improve WUE, ultimately boosting sustainable agricultural productivity by itemizing biomass produced per unit of water used (Fang and Xiong 2015).

Drought resistance in crop species can be accomplished directly or indirectly through trait genetic diversity, which allows for improvement through selective breeding. Marker-assisted selection (MAS) and genomic selection (GS) are the two basic methodologies used in genomic-assisted breeding. The initial stage in MAS is to find molecular markers linked to the target trait, which is required for selection in breeding programs. GS, on the other hand, is based on the building of selection models based on genetic markers found throughout the genome, as well as the selection of genome-estimated breeding values (GEBVs) in breeding populations via phenotyping the training population. For several decades, MAS has been an important component of many crop breeding programs, whereas GS is a relatively new technology that has just recently been applied to crops (Seleiman et al. 2021).

Molecular markers contribute to marker-assisted selection (MAS) by being situated near quantitative trait loci (QTL) or specific genes linked to a certain target trait. These indicators can be used to identify people who have favorable alleles (Varshney et al. 2014). Using accurate and reliable trait evaluations and a dense set of molecular markers, QTL mapping or genome-wide association techniques are used to choose markers that are related to traits. These approaches have been used to find QTLs linked to drought resilience in a variety of crops, including wheat (Kollers et al. 2013), maize (Brown et al. 2011), sorghum (Huang et al. 2010), rice (Morris et al.

2012), soybean (Hwang et al. 2014), pearl millet (Bidinger et al. 2007) and many other crops.

Genomic Selection (GS) uses all available markers to pick elite lines from a population of genome-estimated breeding values (GEBVs), and GS models are used to select elite lines without the necessity for phenotyping. Unlike MAS, knowledge of QTLs is not required for GS (Nakaya and Isobe 2012). Nonetheless, genomic selection (GS) requires more marker data than marker-aided selection (MAS). This increased density is made possible by using low-cost genotyping technologies that cover markers across the entire genome (Hayes and Goddard 2001). The international maize and wheat improvement center (CIMMYT) is currently using GS in the development of drought-resistant maize (Crossa et al. 2014). Similar research efforts are underway in other crops such as sugarcane, legumes, and wheat, with the goal of implementing this strategy to improve drought tolerance (Gouy et al. 2013; Varshney et al. 2013; Rutkoski et al. 2010).

10.5.2 Molecular and Genomic Strategies

Biochemical and molecular components contribute to the initiation of mechanisms that mitigate the harmful consequences of water stress. Transcription, stress-responsive genes (as indicated in Table 10.1), and the hormone abscisic acid are among these variables (Osakabe et al. 2020). In addition to improving drought resistance, breeding programs aim to improve stress management by introducing transgenic expression of several stress-responsive genes (Rai and Rai 2020; Liu et al. 2020). However, overexpression of these genes frequently leads to a decrease in plant growth rate, limiting their practical application. To effectively address these difficulties, it is critical to continue to focus on the molecular and genetic basis of drought resilience (Hussain et al. 2018).

Genomic and related technology methods can aid in the identification of genes that ameliorate the effects of stress, allowing efforts to preserve and incorporate these genes into future breeding programs (Medina et al. 2016). Stress-tolerant genes work at the molecular level and interact with quantitative loci traits, emphasizing the need of studying their interactions and cloning stress-related genes (Nakashima et al. 2014). In the field of genetic engineering, it is commonly agreed that a combined approach including marker-based selection, molecular approaches, and traditional breeding is the most effective option for increasing plant tolerance to abiotic stress (Bhatnagar-Mathura et al. 2008; Cho and Hong 2006).

The clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9 (CRISPR–Cas) system of genome editing is a recently developed molecular technique which has been appreciated for its adaptability and ease of operation. CRISPR–Cas-based genome editing is applied in several economically important crops, including cotton, rice, wheat, maize, soybean, potato, and in biofuel crops (Sami et al. 2021; Tiwari et al. 2021)). CRISPR–Cas system has been proved useful in developing resistance to multiple abiotic environmental stresses, including

Table 10.1 Gene associated with plants' ability to tolerate drought stress

S. no	Crop plant	Target gene	Function	References
1.	Rice (*Oryza sativa*)	*OsDREB*	Specifically induced under cold stress conditions	Aharoni et al. (2004)
2.	Rice (*Oryza sativa*)	*OsERF7*	Predominantly expressed in the root meristem, pericycle, and endodermis	Shou et al. (2004)
3.	Maize (*Zea mays*)	*Maize glossy6 (gl6)*	The protein is involved in trafficking of intracellular cuticular waxes and drought tolerance	Li et al. (2019)
4.	Wheat (*Triticum aestivum*)	*TaLEA3*	Rapid stomatal closure in transgenic plants to tolerate drought	Yang et al. (2018)
5.	Apple (*Malus domestica*)	*MdSHINE*	Confers drought tolerance by regulating wax biosynthesis	Zhang et al. (2019)
6.	Potato (*Solanum tuberosum*)	*StDREB2*	Promotes drought tolerance	El-Esawi and Alayafi (2019)
7	Wheat (*Triticum aestivum*)	*TaNAC69*	Increased tolerance to drought	Seleiman et al. (2021)
8	Maize (*Zea mays*)	*NF-YB2*	It increases yield and photosynthetic rate under drought	Seleiman et al. (2021)
9	Rice (*Oryza sativa*)	*AP37*, *OSNAC10*	Drought tolerance and grain yield increased	Seleiman et al. (2021)
10	Sugarcane (*Saccharum officinarum*)	*SodEFF3*	Increase in resistance to drought	Seleiman et al. (2021)
11	Soybean (*Glycine max*)	*P5C5*	Increased in drought tolerance	Seleiman et al. (2021)
12	Tobacco (*Nicotiana tabacum*)	*HSP70-1*	Drought stress tolerance	Seleiman et al. (2021)

salinity, drought, heavy metals etc. Different types of CRISPR/Cas technology have been successfully used to develop drought tolerance by altering genetic features in diverse plant species. By targeting certain agronomically relevant gene regulators, CRISPR–Cas could significantly improve plant tolerance to drought stress and is able to increase average crop production. For example, it was shown that the maize variants modified using CRISPR method were found to be more tolerant towards drought (Shi et al. 2017). Other such experiments also showed that CRISPR–Cas9 method can be effectively implemented to induce novel allelic modifications for developing drought-tolerant crop varieties. However, relatively few studies have explored the application of CRISPR–Cas-methods to improve crop tolerance of drought stress, compared to other abiotic stresses. The research gaps in development of genome-edited crops are the discovery of target genes, effective delivery of CRISPR machinery to the appropriate cells and regeneration of various crops. Particular attention should be given on drought stress response genes and drought stress-induced transcriptional networks to address the issue of target discovery (Joshi et al. 2020). Additionally, a thorough comparative genome-wide analysis can develop a solid baseline for further identification of the potential target genes in crops (Table 10.1).

10.6 Conclusion

Climate change has led to increased biotic and abiotic stresses, posing serious threats to global food security and plant production sustainability. Drought, an abiotic stress, is particularly concerning due to its adverse impact on plant growth, development, and yield, leading to food insecurity worldwide. Drought stress affects plants throughout their life cycle, from germination to maturity, and disrupts various physiological, metabolic, and biochemical processes, hampering plant productivity. However, plants have developed mechanisms to enhance drought tolerance and mitigate its adverse effects.

To address the challenges posed by drought stress, it is essential to explore untapped adaptive traits in different plant species and incorporate them into genotypes that can tolerate water scarcity without compromising productivity. Breeding technologies offer great potential for improving plant performance under water deficit conditions, and various approaches are being explored for drought adaptation in arid and semi-arid environments. Several strategies can be employed by plants to enhance drought tolerance, including modifying growth patterns, reducing transpiration loss through stomatal conductance alteration and distribution, leaf rolling, adjusting root-to-shoot ratio dynamics, increasing root length increment, accumulating compatible solutes, improving transpiration efficiency, regulating osmotic and hormonal responses, and delaying senescence. To overcome the adverse effects of drought stress, researchers need to work further on developing some innovative methods like changes in breeding strategies, alterations in omics technology or novel approaches related to CRISPR/Cas through which a better understanding can be developed about plant responses to drought stress. This can further potentially increase plant productivity in dry environments, and thus can reduce the threats to global food security.

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