Review

Advancing Drought Tolerance in Plants: Integrating Morphological and Genomic Mechanisms.

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Abstract Drought significantly reduces water availability, negatively affecting critical plant processes and reducing crop productivity. This has serious economic consequences, especially in regions that rely heavily on agriculture. Plants respond to drought stress through intricate biological mechanisms, including changes in metabolite profiles and gene expression, which help mitigate damage and maintain functionality.

Central to these responses are transcription factors, which regulate stress-responsive gene expression by mediating signal transduction pathways. Their role is pivotal in linking drought signals to physiological and molecular adaptations. Understanding these complex networks of physiological, metabolic, and gene regulatory responses is essential for developing crops with improved drought resilience.

Marker-assisted selection (MAS) provides a more efficient method for assessing the value of various genomic regions in crops under stress conditions. Numerous crops contain quantitative trait loci (QTLs) linked to drought tolerance and other traits. The development of detailed molecular linkage maps and MAS techniques has enabled the integration of favorable characteristics, enhancing agricultural resilience to drought. Despite these advancements, challenges persist in achieving accurate and precise QTL identification.

This review incorporates insights into signal transduction for developing drought-resistant crop cultivars or lines. It also explores recent progress in understanding transcription factors (TFs), with a particular focus on their role in orchestrating plant responses to abiotic stress. Additionally, it delves into novel molecular mechanisms underlying their function in stress conditions. These insights are crucial for understanding regulatory processes and developing stress-resistant crop varieties.

Keywords: Plants, Drought tolerance, Morphology, Metabolism, Transcription factors (TFs), Marker-assisted selection (MAS), quantitative trait loci (QTLs),

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1 INTRODUCTION

Global food safety is a key problem universally due to changes in global climate conditions besides the rise in population [1,2]. The global necessity for improved agricultural productivity on marginal rainfed lands is crucial for addressing present and future food security challenges. The impact of climate change, characterized by heightened variability and fluctuation in hydrological patterns, poses a significant threat to agricultural practices, particularly in developing countries. This phenomenon exacerbates various abiotic stress factors for plants [3]. Heat, drought, stress, and salinity significantly affect plant production and yield [1,2]. Drought is an essential and major limitation among the abiotic factors. Drought stress impacts about one-third of all agricultural land globally. Within this affected area, emerging countries account for 33%, developed countries represent 25%, and underdeveloped countries comprise 42%.[4]. The Intergovernmental Panel on Climate Change (IPCC) has determined that the increased concentration of greenhouse gases is likely to cause the subtropical regions to become drier by the end of the century, resulting in widespread drought stress in agriculture [5]. Approximately 75% of the world's water consumption is at risk due to this global water shortage, with irrigation accounting for more than 90% of water use in several developing nations [6].

Plants are generally more vulnerable to extreme environmental conditions compared to other living organisms. They tend to suffer adverse effects when exposed to high levels of environmental stress, which can negatively impact their biochemical and physiological processes [7]. Every stage of plant growth, from seed germination to plant maturity, depends on water, and the lack of it is the main cause of diminished plant productivity by disrupting crucial morphological and biochemical processes [17,18], which significantly causes decreases in food production, which has significant socioeconomic repercussions over the world [8]. Hence, in agriculture, drought refers to a period characterized by a scarcity of precipitation, resulting in impaired crop growth and diminished yields due to either poor rainfall or heightened evaporation rates [9-16]. Furthermore, drought conditions can also negatively impact crop production and plant yield by as much as 50%. [19,20], especially in the reproductive stages of plants which are generally more susceptible to stress, and which can have a significant impact on the yield of numerous important plant species [21]. A reduction in water content by up to 40% has been shown to result in a significant decrease in the yield of both wheat and maize, with reductions of up to 40% and 21%, respectively [22,23]. For example, the production of cowpeas can be significantly impacted by drought stress, with a reduction of up to 68% [24]. 40% of soybean yield loss is caused by drought stress [25]. It also slows down cell division, expands the surface area of the leaves, curtails stem growth, and impedes root propagation [26]. Stresses such as drought and salinity affect the productivity of most field crops to variable degrees, depending on the onset time, duration, and intensity of the stress [27]. Rice (*Oryza sativa*), one of the most important food crops in the world, is very sensitive to drought stress because of its limited adaptation to water-deficit conditions [28,29]. The impact of drought stress on rice seed germination and seedling growth can be observed through changes in the plant's early morphology [24,30-31]. Significant decreases in germination rates and seedling growth are typically seen in conditions of drought stress (DS) [32]. Maize, another essential crop (*Zea mays*), is highly susceptible to water-deficit stress. The soil's water supply heavily influences its pollination and embryo development processes during and after flowering [22,33]. In addition, drought disrupts the water balance and impairs the cellular level's metabolic process, including respiration and ATP production, ultimately affecting membrane transport. These consequences can result in poor seed germination [30].

Plant drought resistance includes four major mechanisms: drought avoidance (DA) (or ‘‘shoot dehydration avoidance’’ in some literature), drought tolerance (DT), drought escape (DE), and drought recovery (DR). Plants respond to drought stress by producing a variety of stress signals, which are processed and interpreted by their defense systems. To manage drought stress, plants employ a range of strategies that can be broadly categorized into morphological, physiological, biochemical, and molecular responses. These mechanisms help plants survive and reproduce under water-limited conditions. One of the structural changes in plants that are critical to responding to drought stress ranges from morphological adaptations (decline in growth rate, deep rooting system, and modification of root-to-shoot ratio for desiccation avoidance) [34,35]; as well as physiological and metabolic responses [36]; include reduced Transpiration by closing stomata [37, 38]. Osmotic adjustments include the accumulation of osmolytes like proline, sugars, and ions [39]; to maintain cell turgor and prevent dehydration.

Furthermore, biochemicals are one of the strategies of plant's defense by enhancing the activity of enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidases to mitigate oxidative damage caused by reactive oxygen species (ROS) [40,41]. Also, increased levels of abscisic acid (ABA) signal stomatal closure and initiate other stress responses [42].
Signaling pathways by activation of signaling molecules like calcium ions (Ca^{2+}), nitric oxide (NO), and reactive oxygen species (ROS) to coordinate stress responses [43].

In addition, one of the most significant strategies to face drought stress is the molecular response that includes Stress-Responsive Genes, such as the upregulation of dehydration-responsive element-binding (DREB) and other transcription factors that regulate drought-tolerance genes [44]. Also, the production of protective Proteins, for example, synthesis of heat shock proteins (HSPs) [45], late embryogenesis abundant (LEA) proteins [46], and aquaporins to protect cells and facilitate water transport.

This study offers valuable insights into the critical changes and mechanisms that plants employ to adapt to and withstand drought stress across multiple levels. It emphasizes the significant alterations occurring at the morphological, biochemical, and molecular levels. By identifying key genes and characterizing the unique features of genetic regulatory networks, the review sheds light on how plants coordinate their responses to drought. In addition, it provides comprehensive and a deeper understanding of the intricate processes that underlie plant adaptation, including the regulation of gene expression, signal transduction pathways, and the activation of stress-responsive metabolic and physiological pathways.

Physiological and Morphological Responses to Drought Stress

The ability of a plant to achieve its maximum economic yield despite water shortage is referred to as drought resistance [16]. To resist drought, plants have developed a wide range of morphological and physiological response mechanisms. As explained by (Kumar et al, 2016) ,it is a trait that is influenced by a multitude of factors, including morphological, biochemical, and physiological responses that are interconnected and subject to change [47]. There are two avoidance strategies that plants employ often referred to as water-saving and water-spending strategies. These strategies include "drought tolerance" (i.e., the capacity to sustain physiological processes at decreasing leaf water potentials) and "drought avoidance" (i.e., the capacity to prevent or delay the decline of leaf water potential during drought) [10,48,49]. According to (Benjamin and Nielsen,2006) [50]; (Praba et al., 2009) [51], drought stress significantly impacts various physiological and biochemical characteristics, including growth, yield, membrane integrity, pigment composition, osmotic adjustment, water relations, and photosynthetic activity. Among its primary effects are impaired seed germination and poor stand establishment [52]. One of the physiological traits is osmotic adjustment, a low turgor loss point, and reduced susceptibility to cavitation are critical factors contributing to drought tolerance [48]. On the other hand, drought-resistant plants may rely on water-conservation mechanisms, including traits like early stomatal closure and foliar abscission [48, 53], or on traits that enhance water acquisition, such as the development of deep root systems and elevated plant hydraulic conductivity, enabling rapid water uptake from the soil to compensate for transportation water losses [54, 55].
Additionally, reducing turgor pressure under drought conditions severely impacts cell development, one of the most sensitive physiological processes. Cell growth, driven by mitotic activity in meristematic regions and subsequent proliferation of daughter cells, is disrupted under severe water deficits due to inhibited water transport from the xylem to elongating cells, thereby restricting cell elongation [56]. This disruption results in impaired cell elongation and expansion, ultimately reducing growth and yield-related traits. Additionally, defective mitotic processes under drought stress further contribute to these developmental impairments [8].

Numerous investigations have identified

characteristics that appearance or presence is connected to a plant's capacity to withstand drought. Among them, characteristics like small plant measurement, small leaf area, early maturity, and delayed stomatal closure diminish the potential yield and total seasonal transpiration [57,58].

Decreased soil water potential leads to a reduction in both the number of leaves per plant and the size and lifespan of individual leaves. Leaf expansion is influenced by factors such as temperature, the availability of growth resources, and leaf turgor pressure.

(Rucker et al, 1995) claimed that drought-induced reductions in leaf areas are caused by a reduction in photosynthesis, which inhibits leaf development [59]. According to (Zhu et al., 2020) the decreased water potential that results from drought stress is the cause of the decrease in leaf growth [60]. The impairment of water transportation from the xylem to another cell, as a result of inadequate water supply and subsequent reduction in turgor pressure, can lead to suboptimal growth of cells and reduced leaf area in plants [8]. The anatomical structure and ultra-structure of a leaf undergo modifications in response to drought stress, as observed by [61]. The reported modifications include a decrease in leaf size, a reduction in stomata count, the development of a thick cell wall, the occurrence of cutinization on the leaf surface, and suboptimal growth of the conducting system [16].

The growth-related characteristics of maize, including plant height, leaf area, number of leaves per plant, cob length, and shoot fresh and dry weight per plant, have been significantly affected by the drought. Additionally, (Kamara et al, 2003) revealed a lack of water at different phases of maize growth decreased the amount of biomass accumulated during the grain-filling stage by 34%, at maturity by 21%, and at the silking stage by 37%[62]. Furthermore, shortage of water leads to a substantial decrease in crop plant yield traits, most likely due to a disruption in the properties of leaf gas exchange, which limits the size of source and sink tissues and reduces phloem loading, assimilate translocation, and dry matter portioning [63]. The main way that drought stress reduces the formation of dry matter is by preventing the growth and development of leaves, which in turn results in less light being intercepted [64]. Also, stomatal closure is caused by low water content in the soil, plant yield and production components may be diminished during drought [65- 67]. Numerous studies have demonstrated that stomata or non-stomatal mechanisms reduce photosynthetic activity under drought stress [68-70]. Stomata are primarily responsible for water loss and CO2 absorbability, and one of the first responses to drought stress is stomatal closure, which reduces the rate of photosynthesis by depriving the leaves of CO2 and reducing photosynthetic carbon absorption in favor of photorespiration [71].

It is generally agreed that there is an extensive correlation between leaf water status and stomatal conductance. Even when there is drought stress, there is always transpiration conductance and leaf water potential. It is now apparent that stomatal closure is the consequence of drought-induced root-to-leaf communication, which is facilitated by soil drying through the transpiration stream. The "non-stomatal" mechanisms include modifications to the synthesis of chlorophyll, structural and functional alterations in chloroplasts, and disruptions to the assimilate accumulation, transport, and distribution processes [68-70].

A typical outcome of drought during blossoming is barrenness. Reduced assimilate flow to the developing ear below a threshold level required to maintain good grain development was a significant contributing factor, however, it was not the only one [72].

Moreover, two significant traits that are commonly observed in plants under drought stress include leaf rolling and the onset of early senescence [73]. Many leaf attributes have been employed to evaluate varieties with drought tolerance, including greater flag leaf area, leaf area index, leaf water content relative to the weight of the dry matter, and leaf pigment content [63,8,31]. In another study, it has been reported that several cereal crops exhibit certain morphological traits to cope with drought conditions, such as rolling their leaves, expanding green flag leaf area, becoming glaucous, displaying increased shoot vigor, exhibiting stomatal conductance, utilizing transpiration cooling, maintaining membrane stability, maturing early, displaying root vigor, and adopting specific architectural features [74]. Although crop plants have developed various physiological mechanisms to cope with drought, their specific strategies include adjusting their osmoprotectant accumulation, chlorophyll content, photosynthetic rate, **Table. 1** ABA accumulation, soluble sugar content, and generation of reactive oxygen species (ROS) [75].

One of the essential features of plants is the roots are crucial for improving crop yield in dry conditions. The formation and composition of the rice root system are crucial in determining the function of crops under water stress. The amount of rice produced under conditions of water scarcity can be predicted by considering the dry mass of the roots and their length [76]**.** A wide range of responses were observed concerning root growth characteristics in the presence of water stress. According to (Manivannan et al, 2007), an increase in the length of rice roots was noticed during drought stress due to the elevation of abscisic acid concentration in the roots [77]. Typically, rice varieties with deep and extensive root systems are more resilient to drought conditions [78, 79]. Rice genotypes with deep and widespread root systems, coarse roots, the capacity to produce many branches, and a high ratio of roots to shoots are strongly associated with drought tolerance [79]. The morphophysiological traits of rice roots significantly influence shoot growth and overall grain yield in conditions of drought stress, as demonstrated by (Kim et al., 2020) [79].

Photosynthesis Responses to Drought Stress

Photosynthesis is a central metabolic process that plays a significant role in determining the growth and production of crops. It is also affected by water deficit or drought stress, which can alter the normal rate of photosynthesis and the characteristics of gas exchange in plants [60]. Under the environmental conditions of limited water, stomata close, which reduces the amount of carbon dioxide entering leaves, leading to a need for additional electrons to produce reactive oxygen species [63, 80]. The decline in photosynthesis is influenced by various factors including diminished leaf gas exchange, a drop in turgor pressure, reduced CO2 assimilation, and stomatal closure **Table. 1**. These elements ultimately harm the photosynthetic apparatus, as shown by research [60,63,81]. The ability of leaves to carry out photosynthesis and the accessibility of water to the root zone are crucial elements that can negatively impact yield in susceptible rice varieties when exposed to drought stress. These factors play a significant role in the growth and development of rice plants, particularly during periods of water scarcity [60]. Drought stress leads to disparities in the acquisition and utilization of light, as well as diminution and impairment of Rubisco activity, pigments, and photosynthetic machinery [63]**,** which results in a decline in photosynthesis. Water stress adversely affects the normal functioning of PSI and PSII [31, 82]

The function of PSII is crucial for the process of reducing substances and creating ATP. Numerous in vivo investigations have shown that drought can cause a significant decrease in the oxygen evolution centers of photosystems, leading to the inhibition of the electron transport chain and the eventual inactivation of PSII [31,80]. Chlorophyll, which is a type of plant pigment, is essential for photosynthesis, as it helps capture light and produce reducing powers [78]**.** Water scarcity results in a decrease in the capacity of mesophyll cells to utilize the carbon dioxide present in the atmosphere. Consequently, the quantity of functional chlorophyll decreases **Table. 1** [83].

In rice plants subjected to water stress, the decrease in chlorophyll levels and the lowest amount of photosystem II (PSII) quantum yields (Fv/Fm) are reported [31,60,80] Carotenoids, which are crucial for photoprotection, are also utilized as precursors in guiding growth signals for plants in stressful conditions. As a result, researchers in plant biology are currently giving special attention to increasing carotenoid levels in plants through breeding or genetic engineering [84].

Signal transduction pathways and Metabolic Responses

This stress triggers a series of responses, such as the recognition of water shortage, initiation of signaling pathways, and adjustments in transcription, metabolism, and regulatory components, all of which contribute to enhancing the plant's resilience against drought stress [85].

Environmental droughts are detected by sensors that are membrane-bound to identify environmental drought conditions. This detection initiates various signal transduction pathways, ultimately activating drought-responsive genes. These genes encode proteins that confer appropriate functions and enhance tolerance to drought stress. [86,87]. Integral membrane proteins, including membrane-anchored receptor-like kinases (RLKs), channels, and other transporters, may be able to detect this alteration. Key cascading events are associated with reactive oxygen species (ROS) and calcium ions (Ca2+). Various plant hormones, including salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA), and ethylene (ET), act as powerful secondary messengers that coordinate signal transduction pathways during stress responses. These signaling molecules initiate multiple concurrent transduction cascades, which often involve the contribution of protein kinases and phosphatases [88]. However, it is technically very difficult to show that a protein or other macromolecule acts as a sensor for a physical signal (such as a change in temperature, ion concentration, or osmotic pressure), and even for commonly used osmosensors or temperature sensors in bacterial, yeast, or mammalian systems, there is no direct experimental evidence.

A wide range of metabolites can hyper accumulate in plants as a result of environmental stressors such as drought, salt, and high temperatures [89,90]. Plants produce primary metabolites (PMs) and secondary metabolites (SMs) to combat a range of adverse physiological changes brought on by stresses [91-93]. The growth and development of plants depend on metabolites, which are involved in cell signaling, energy storage, membrane construction, scaffolding, and the distribution of resources across the entire plant under stress [94]. Plant metabolism is disrupted by drought for a variety of reasons, including the inhibition of metabolic enzymes, a lack of substrate, an excess of demand for certain chemicals, and many more [95].

Several analyses have advanced our knowledge of how many plant species regulate their metabolites in response to various environmental stressors, such as drought, salt, heat, cold, and light stress [96,97]. Methodologies for metabolite profiling have been widely utilized to assess metabolite levels in a specific metabolite class or pathway to describe the biochemical responses to DS in plants [98,99].

The analytical techniques employed to identify specific categories of metabolites in different plant species under DS include high-performance liquid chromatography (HPLC), nuclear magnetic resonance (NMR), liquid chromatography-mass spectrometry (LC-MS), capillary electrophoresis-mass spectrometry (CE-MSgas),and chromatography-mass spectrometry (GC-MS) [100,101]. Metabolomic studies can relate the genotypic and phenotypic alterations in plants during DS and explore and identify important distinctions between DS-tolerant and DS-sensitive plant species/genotypes [102].

Plant development processes, photosynthesis, and respiration depend on primary metabolites such as sugars, polyols, amino acids, and lipids, which also help plants adapt to and recover from drought stress [103]. Under drought circumstances, they are crucial for preserving osmotic balance, managing ion transport, stabilizing cell membranes, and controlling cell turgor pressure [104]. During DS, *Z. mays's* glutathione and urea cycles, as well as its metabolism of carbohydrates and fats, are essential for osmoprotection, membrane upkeep, and antioxidant defense [105].

There are two primary approaches to comprehending metabolic reprogramming in plants under abiotic stress: non-targeted and targeted [106-108]. The most prevalent metabolites in plants under different environmental stressors are summarized using non-targeted metabolomics. When plants are subjected to different environmental stressors, targeted metabolomics finds, quantifies, and examines known [109,110]. The significance of metabolic reprogramming, including the control and buildup of PM and SM levels in plants under DS and biotechnological implications for DS management of agricultural crop plants, may therefore be demonstrated by metabolomics investigations [111,112].

Glycine and myoinositol levels were reported to be significantly correlated with grain yield by Obata et al, 2015 [113], who used GC-MS to investigate the leaf blade tissue of *Z. mays* under DS.

In *Zea mays* [114] and *Oryza sativa,* trehalose levels decreased. Sugar alcohols (arabitol and galactitol) and sugars (glucose, galactose, fructose, and maltose) accumulated in *Lotus japonicus* during DS [114]. Sugars (fructose, cellobiose, galactose, lactose, and sedoheptulose) and sugar alcohols (myoinositol, ribitol, and xylitol) were significantly upregulated in Samsorg 17 compared to Samsorg according to Ogbaga et al (2016)'s study of two drought-contrasting sorghum (*Sorghum bicolor*) cultivars (Samsorg 17 and 40) under DS [114].

Differential accumulation of metabolites occurred in two drought-contrasting chickpeas (*Cicer arietinum* L.) genotypes using the UPLC-HRMS-based untargeted metabolic profiling approach [115]. Other PMs (such as proline, arginine, histidine, isoleucine, and tryptophan) increased in the tolerant chickpea variety's leaves under DS, but both genotypes had decreases in alanine, ketoglutaric acid, GABA, choline, tyrosine, glucosamine, adenosine, guanine, and aspartic acid [115]. In comparison to control plants, wheat (*Triticum aestivum*) subjected to DS has higher levels of several vital metabolites, including sugars, AAs, and GABA [116]. Likewise, in response to DS, wheat genotypes that were drought-tolerant and drought-sensitive showed elevated levels of proline, methionine, lysine, and arginine contents [117]. One or more of *Hordeum vulgare's* organs showed a notable production of metabolites under DS [118]. During DS, proline increased in all organs (fifth leaf, awn, lemma, and palea), but valine was markedly elevated in the fifth leaf, awn, and lemma [118]**.** Although the majority of research has proven the involvement of amino acids as osmoprotectants, additional metabolites such as organic acids, sugars, and phenolic compounds have been suggested to be important for abiotic stress in a variety of plants [119,120]. While proline catabolism improves during stress recovery, proline synthesis generally seems to be activated by stressful situations [121].

Table 1 Physiological and biochemical responses of plants under drought stress (modified Kumar, 2018) [122]

No.	Plant traits	Yield-related effects on plant	Variation in stress	Ref.
1	Plant dry weight, total leaf area, and net photosynthesis production	After being watered, to restore the net photosynthesis	Cultivars that are resistant to drought stress	[123]
2	Osmolality, and amino acid	Under stress, alterations in plant metabolism and water potential result in a reduction in yield.	Water shortage raises amino acid and osmolality levels.	[124]
3	The actions of peroxidase and electrolyte loss	lower emerging success and an increase in water stress	Chlorophyll and relative water content fall under stress, whereas phenol and peroxidase activity rise.	[125]
4	The amount of chlorophyll and membrane stability	decreased total carotenoid concentration, relative water content, and membrane stability across all cultivars, but total chlorophyll content rose.	Pod development stage water deficiency stress was shown to be more harmful than pegging stage stress.	[126]
5	Antioxidative enzymes, relative water content in the leaves, and root water absorption	Under water stress conditions, it increases tuber production and antioxidative enzyme activity.	Certain cultivars exhibit increased drought resistance while under stress.	[127]
6	Degree of transpiration	Variability in stomatal conductance and leaf area	Tolerance is rare in landrace species.	[128]
7	Rate of photosynthesis and isotopes of carbon in leaves	Stomatal conductance enhances water-use efficiency.	Improve the ability to tolerate water deficits	[129]
8	Grain yield, leaf area index, and relative water content	In a chosen genotype, total biomass and yield increase during water deficiency	Adaptable to stress from water shortage	[130]
9	Efficiency of consumption of water	Average yield increase during the case of a water deficiency	Drought tolerant	[131]
10	rate of photosynthetic activity and conductance of stomatal cells	Increased biomass gain and a high degree of photosynthetic rate under drought	Resistance in times of stress	[132, 133]
13	Root length and leaf area	Increased root-to-above-ground ratio and more leaf area	Adapt to extreme drought conditions and survive	[134]
14	Photosynthetic capability, stomatal conductance, and fresh and dry weights of the shoots	Shoot fresh and dry weights, stomatal conductance, and photosynthetic capacity all drop less.	Shows drought stress tolerance in selected species	[135]

Molecular Responses to Drought Tolerance

While drought tolerance is a result of many physiological, metabolic, and cellular processes, it also arises at the molecular level through the induction or repression of multiple genes that lead to the buildup of different osmolytes, improved antioxidant systems, and decreased transpiration [136]. Activating a multitude of genes with diverse functions triggers the plant's physiological and biochemical responses to drought stress [137].

The development of "Omics"-based techniques, including transcriptomics, proteomics, metabolomics, interactomics, and phenomics in several model species, has contributed significantly to new experimental knowledge in the post-genomic age. These methods have laid the groundwork for "Functional Genomics," which seeks to identify genes and define their roles [107].

Numerous researchers across the globe have undertaken extensive research to improve the drought tolerance of the crucial crop by identifying and characterizing suitable dehydration-responsive candidate genes. These genes are categorized as either functional genes or regulatory genes. Functional genes like those that encode Numerous enzymes that are engaged in the creation of protective metabolites, transporters/channel proteins, antioxidative enzymes, genes involved in lipid biosynthesis, etc., support distinct mechanisms that help plants survive stress and recover from it. Regulatory proteins, including transcription factors (TFs), alternative splicing factors, protein kinases, stress receptors, and parts of the machinery that break down proteins, are encoded by regulatory genes. These regulate signal transduction pathways and alter the expression and by-products of many genes linked to stress [138-142].

Molecular procedures associated with drought tolerance are typically examined within two primary categories. According to(Joshi et al, 2016),[143] these important genes primarily code for proteins with metabolic or regulatory functions, including those involved in detoxification, osmolyte biosynthesis, proteolysis of cellular substrates, water channels, ion transporters, heat shock protein (HSP), membrane-stabilizing proteins, chaperones, and late embryogenesis abundant (LEA) protein [144]; which help to increase the water-binding capacity of cells by functioning in water channels.

TFs (NAC,AREB, AP2/ERF, MYC, MYB, and bZIP), calcium-dependent protein kinases (CDPK), signaling protein kinases (mitogen-activated protein kinases, or MAKK), ribosomal protein kinases, receptor protein kinases, transcription regulation protein kinases), and protein phosphatases (phospholipase and phosphoesterases) are the main components of the regulatory class, on the other hand, which synchronizes signal transmission and gene expression during stress responses [145,146]. Through their regulation of downstream stress-responsive genes, some of these regulatory genes, including TF have been demonstrated to be essential for several abiotic stress reactions. Alteration of the expression of these regulatory genes can therefore have a major impact on plant stress tolerance as they also regulate a large number of downstream stress-responsive genes at a given time [147].

Molecular analyses of signal transduction pathways reveal a significant correlation between changes in turgor pressure and the biosynthesis of the stress hormone abscisic acid (ABA), which subsequently triggers the activation of stress-responsive genes [149]. This process involves the engagement of various protein molecules critical to stress signaling pathways, including transcription factors (TFs), enzymes, molecular chaperones, and metabolites. These proteins contribute to the intricate signaling cascades that enable plants to cope with water deficit stress. Additionally, a diverse array of signaling molecules has been identified as pivotal components in stress perception and signal transduction pathways. These include ABA, reactive oxygen species (ROS), hydrogen peroxide (H2O2), nitric oxide (NO), calcium ions (Ca^{2+}), and polyamines (PAs), among others, which collectively regulate stress responses and adaptation mechanisms in plants [149]. Despite extensive research efforts, relatively few potential sensor proteins have been conclusively identified.

The primary challenge lies in the functional redundancy of genes encoding these sensor proteins, where the loss of function in one gene is often compensated by others, preventing noticeable stress-response phenotypes. This redundancy complicates the identification and characterization of critical sensor genes and highlights the complexity of plant stress signaling networks [150]

Abscisic acid, or ABA, is a key modulator of many adaptable characteristics of plant developmental enhancements, including root growth, flower commencement, seed dormancy, germination, and embryo maturation. Additionally, it has been demonstrated that the ABA-independent regulatory mechanism controls drought-induced gene expression [145,151]. Under water-deficit conditions, the phytohormone abscisic acid (ABA) is reported to be abundant, leading to stomatal closure and the alteration of expression of various stress-related genes [152]. Several TF genes have been found to respond to drought stress through pathways that are either dependent or independent of ABA [145]. That means although many genes involved in the ABA signaling system are responsive to drought, the majority of genes activated by drought do not respond to ABA treatment, suggesting the existence of ABA-independent drought-response pathways [153].

(Grill and Himmelbach,1998), explained these two systems for stress response in plants: the abscisic acid-dependent; and the abscisic acid-independent, which are activated by various TFs, including ABA-responsive element binding protein (AREB proteins), ABF proteins (ABRE-binding factor), DREB factors (dehydration responsive element binding factors), MYB/MYC proteins, and NAC proteins (NAM, ATAF1-Two and CUC domains)[154]. Moreover, other TFs provide drought tolerance via ABA-dependent pathways, such as bZIP [155, 156] NAC [155,157], ERF, HSF, ARF [158], WRKY, C2H2 [157], and trihelix [159]; control the drought response at the molecular level by regulating gene expression in metabolic pathways [160, 161]. TFs act as vital molecular switches that allow plants to adapt to abiotic stress and regulate their developmental process in the face of adversity [161, 143].

The distinctive TFBS of the plant-specific TFs defines their families. About 1500 likely TFs from about 30 TF families were found when the *Arabidopsis thaliana* (Arabidopsis) genome sequencing was finished [161,162]. Since no members of these families have been found in other eukaryotic lineages, around half of them were deemed to be plant specific. Specifically, (Yamasaki et al, 2013)'s recent investigation of plant TFBS three-dimensional structures showed that they most likely arose from endonucleases linked to transposable elements [163]. After being discovered in eukaryotes, TFBSs had significant growth in plants, gaining additional complexity and roles. Ten percent or so of plant genes encode TFs [164], which take part in different stages for a specific purpose.

Various stress-responsive transcription factors (TFs) typically operate independently, there is potential for some degree of interaction or cross-talk between them. Under stress conditions, numerous TF families that are relevant to the drought stress response have been discovered in recent years [165]; including CBF, DREB, MYB, ABF, AREB, ABA, SNF1-related kinase 2 SnRK2, NAC, and WRKY [166]. These fundamental amino acids enable plants to resist abiotic stress [167]; and directly regulate the expression of genes linked to stress responses by functioning as molecular switches during signal transduction. Transcription factors (TFs) work together with other binding sites to activate plant genes [168,169]. They bind to the cis-acting elements that are present in the upstream regions of all gene promoters [170]. Moreover, TFs either activate or suppress the activity of the DNA polymerase enzyme and play a crucial role in gene expression [171].

In recent times, Wen et al, 2019 stated the tolerant response of an important tree species, *Betula platyphylla* (birch), to drought stress[172] . They identified 2917 genes related to drought stress through RNA-Seq method. Among these genes, MYB, MYC, ERF, bZIP, and WRKY families have already been implicated in the regulation of stress responses [162,173]. In Arabidopsis, researchers have identified over 34 families and approximately 1533 transcription factors (TFs), which have been categorized [174]. As a result, these transcription factors are attractive targets for gene regulation and manipulation of the regulatory elements, which may be beneficial under abiotic stresses. By up-regulating many natural stress-responsive pathways, the CBF (C-Repeat Binding Factor) genes provide abiotic stress tolerance [175,176]. ABA response element binding factor 3 (ABF3) and C-repeat binding factor/Dehydration responsive element binding protein (DREB1A) are overexpressed in transgenic rice with enhanced resistance to extreme salinity and drought, but comparatively low resistance to exposure to cold temperatures [177].

Table 2. List of genes and their functions associated with drought tolerance.

Name	characterization	Type of tissue	function	Ref.
EcNAC67	NAC (NAM, ATAF1/2, and CUC2) family	Roots Leaf	influence plant developmental processes such as leaf senescence, root development, and vascular differentiation.	[178, 180]
DRO1 (Deeper Rooting 1)	IAA (Aux/IAA) gene family	Root	Deep rooting facilitated by DRO1 enhances the plant's ability to survive and maintain productivity during water-limited conditions	[181 ,182]
DsM1	(Drought Stress Mitigating 1) is a Raf-like mitogen-activated protein kinase kinase kinase (MAPKKK) gene.	Stamen, pistil, mature leaves and roots	DsM1 contributes to drought tolerance by enhancing ROS scavenging activity, reducing oxidative damage during drought stress. It acts in an abscisic acid (ABA)-independent signaling pathway, which is crucial for drought adaptation.	[183, 184]
PYL/RCAR5	OsPYL/RCAR5 is a key ABA (abscisic acid) receptor in rice (*Oryza sativa*), part of the PYL/RCAR family involved in ABA signaling	Leaf blade, higher root and shoot mass	It induces stomatal closure by activating ABA signaling pathways -By controlling water balance and stomatal conductance -OsPYL/RCAR5 helps maintain leaf fresh weight, contributing to drought resilience and overall plant health. - It interacts with PP2C (type 2C protein phosphatases) to release SnRK2 (SNF1-related kinase 2), which activates downstream genes involved in stress responses, including those for ROS scavenging and osmotic adjustment. - OsPYL/RCAR5 and EcNAC67 delay leaf rolling and induce higher root and shoot mass in rice under water deficit conditions	[185 -186]
DREB1F	Transcription factor in the DREB (dehydration-responsive element-binding) family.	Almost all tissues, but higher in callus and panicle Root morphological adaptations	contributes to the ABA-dependent signaling pathway, coordinating stress-responsive gene expression to enhance plant resilience.	[187 .188]
DREB2B	Transcription factor in the DREB (dehydration-responsive element-binding) family.	Leaf-sheath, Root tissues Root morphological adaptations	dehydration-responsive element (DRE), is an essential *cis*-acting element for the regulation of *RD29A* induction in the ABA-independent response to dehydration	[189-190]
CYP735A	family of cytochrome P450 monooxygenases	Enhancing shoot growth and yield. Improving stress tolerance. Controlling root architecture to optimize nutrient uptake Shoot and root growth, - leaf-cell dividing	CYP735A enzymes are key players in the biosynthetic pathway of trans-zeatin, linking cytokinin production to plant growth and environmental adaptation for drought stress Maintains cytokinin level	[191]
EcNAC67	It is a member of the NAC (NAM, ATAF1/2, and CUC2) transcription factor family	Leaves and roots	It is particularly involved in the activation of stress-responsive genes, such as those associated with antioxidant defense, osmolyte production, or structural adaptations to stress. Increases relative water content in leaves, delays leaf rolling symptoms, ensure better stomatal regulation during dehydration, and maintains higher root and shoot biomass	[178]
NAC5	It is a member of the NAC (NAM, ATAF1/2, and CUC2) transcription factor family A new ABA-dependent transcription factor	flag leaves Grain filling	They directly regulate the expression of the genes linked to stress responses and improve drought resistance by functioning as molecular switches during signal transduction.	[195]
NAC46	The NAC (NAM, ATAF1/ATAF2, and CUC2) transcription factors belong to a large family of plant specific transcription factors	Plant root and shoot Leaves	activates ROS-scavenging enzymes and enhances root formation	[192]
NAC51	It is a member of the NAC (NAM, ATAF1/2, and	lateral root; secondary wall	-NAC transcription factors are often involved in maintaining	[193]

	CUC2) transcription factor family	thickening, plant development, flowering, senescence, and seed quality, anther dehiscence,	cellular homeostasis during unfavorable conditions. -improve structural traits like wood quality.	
SNAC1	SNAC1 (Stress-responsive NAC1)	callus, root, ligule, stamen, and pistil under normal growth conditions,	Enhances spikelet fertility	[194 -196]
LEA3-1	is a member of the Late Embryogenesis Abundant (LEA) protein family,	development, Late embryogenesis is found in roots, stems, and other organs throughout the plant growth phase.	Overexpression of LEA3-1 in transgenic rice and other plants has shown: Improved drought tolerance. Better survival under water-limited conditions. Plants with high LEA3-1 expression display less wilting, better root development, and higher chlorophyll retention under stress. LEA3-1 may also play a role in reducing oxidative damage during stress by mitigating the effects of reactive oxygen species (ROS). Enhances grain yield	[197 -199]
OsbZIP46	It is a member of the bZIP (basic leucine zipper) transcription factor family in rice (*Oryza sativa*).	The lengths of the shoot and root	It is involved in the ABA signaling pathway, which is essential for stomatal closure, reducing water loss, and maintaining cellular homeostasis under drought stress.	[200]
OsMIOX	It is a Myo-inositol oxygenase enzyme in rice	Grain -early growth stages. plays a central role in inositol metabolism, linking it to stress tolerance, cell wall biosynthesis, antioxidant defense.	OsMIOX contributes to drought and salinity tolerance by modulating inositol metabolism, which influences osmotic balance and reactive oxygen species (ROS) detoxification. It enhances the production of metabolites involved in osmoregulation and stress protection, such as compatible solutes.	[201]
OsbZIP33	It is a basic leucine zipper (bZIP) transcription factor in rice (*Oryza sativa*), part of a large family of transcription factors	seed development Root-seed	OsbZIP33 activates or represses genes involved in: Osmo protectant synthesis: Compounds like proline or sugars that help maintain cellular osmotic balance. Antioxidant defense: Enzymes and metabolites that reduce oxidative damage caused by stress-induced reactive oxygen species (ROS). Stomatal closure: Regulating water loss during drought stress.	[202]
CBF3	C-Repeat Binding Factor) genes		under drought stress showed increased antioxidant activity and photosynthetic rate in transgenic *Salvia miltiorrhiza* plants.	[203]
GmMYB84	MYB	Root, Flower, and	enhances the response to drought stress and encourages root development Soybean roots and flowers	[204]
ZAT18	Zinc finger	Leaves, Stems, siliques	Positive drought stress regulator in Arabidopsis	[205]
GmYABBY10	YABBY	germination root, Seedling,	Highly sensitive to drought in Soybean	[206]
OsC3H10	Zinc finger	Seeds	Response to drought in Rice	[207]
GmNAC5	NAC	Seeds	Involved in seed development and abiotic in soybean	[208]
OsMYB4	MYB	Leaves, root, stem, flower, seed	Improved physiological and biochemical adaptationRice/Transgenic Apple	[209]
ARS1	MYB	Root, flower, leaves Tomato	Stomatal closure	[210]

The final stage involves the expression of functional genes that play roles in processes on the morphological level such as oxidative stress mitigation, leaf senescence, stomatal closure, or indirectly influencing regulatory genes that participate in signaling pathways and transcriptional regulation of gene expression **Table. 3** [211,212]
The complexity and makeup of the target genes that are found in the genome, as well as the transcription factor's ability to either activate or repress each target gene, **Figure 1** may be the cause of these functional variations [156].

Several genes related to DS at the transcriptional level have been investigated in microarray and real-time polymerase chain reaction (RT-PCR) studies [213-217,85,160,143]. Functional validation revealed that these genes protect against dehydration stress through stress perception, signal transduction, and transcriptional regulatory networks responding to drought tolerance **Table. 3** [218,219]. Furthermore, gene expression profiles are frequently used in conjunction with qRT-PCR to investigate drought stress tolerance mechanisms. For instance, while comparing the differentially expressed genes (DEGs) between control plants and PEG-treated *Reaumuria soongorica*, Liu et al, 2014 [220] discovered that 379 genes were up-regulated and 946 genes were down-regulated under drought stress. *R.*

soongorica may be able to survive drought stress by activating effective signal transduction pathways and strengthening the defense of helpful proteins to restore cellular homeostasis, based on an examination of these DEGs [220].

Gene expression in maize lines that were drought-tolerant and drought-sensitive was compared under moderate drought, severe drought, and enough water (controls). The tolerant line's genotype-specific response of TFs and its permanent genotypically deferential expression of TFs may be important elements in maize's improved drought tolerance, according to further transcription factor study between these two lines [221].

Kumar et al, 2019; collected genome-wide transcriptome data of stressed indica and japonica rice cultivars [222]. Data analysis revealed that drought stress triggered responses from biological systems and related regulatory circuits. Candidate stress-responsive genes and a number of biological processes that are both similar and distinct across tolerant and sensitive types were found by examining DEGs [223].

Dalal et al, 2018; looked into the molecular mechanism of drought-induced root development in wheat using RNA-Seq [224]. They discovered that during drought stress, the root development of two wheat genotypes—Raj3765 and HD2329—varies, with 2783 and 2638 DEGs, respectively [224]. According to their findings, drought-induced root development in wheat requires a complicated interplay between hormones, ROS metabolism, cellular tolerance, and cell wall formation. Fox et al, 2018, investigated the dynamics of the physiological and molecular responses in *Pinus halepensis* under drought stress circumstances using transcriptome analysis at six physiological phases [225]. Their results showed that drought stress was responsible for the abscisic acid response, ROS scavenging through ASA-independent thiol-mediated pathways, the accumulation of heat shock proteins, thaumatin, exordium, and chlorophyll degradation [225].

In reaction to drought, plants modify the expression of certain genes and build up osmo-active substances. It is commonly recognized that plants overproduce phytohormones, including chaperone proteins, oxygen scavenger radicals, and abscisic acid [226]. Plants are known to overproduce phytohormones, including oxygen scavenger radicals, abscisic acid, and chaperone proteins [198]. Numerous metabolic, defensive, and physiological networks are stimulated by these chemicals. More specifically, the molecular metabolic system is made up of several signaling proteins, regulatory transcriptional factors, and functional genes that work together to achieve the desired outcome **Table. 3**[226].

Additionally, the ethylene-responsive factor and myeloblastosis oncogene families of transcription factors were found to be the most abundant. Also, researchers have reported that BpERF2 and BpMYB102 transcription factors play a crucial role in enhancing plant resistance to drought **Table. 3** [172]. These two TFs activate various other stress-related genes, ultimately providing drought tolerance. (Sakuma et al, 2002) [227] identified different types of DREBs transcription factors in the model Arabidopsis plant **Table. 3**. They proposed that DREB2A and DREB1A attach to a particular six-nucleotide sequence (A/GCC GAC) of DRE, increasing drought and cold tolerance in Arabidopsis [177,207,200,227-230]. However, the specificity of these transcription factors varies with changes in the second and third nucleotides in the sequence (A/GCC GAC) of DRE. They also categorized these proteins into different groups, such as the AP-2 subfamily, RAV subfamily, DREB subfamily, ERF subfamily, and others. This information is supported by [231]**.** APETALA2/ERF (AP2/ERF) is known as a broad family of TFs and protein kinases that are involved in regulating many biological processes in plants. It is widely known how the AP2/ERF family reacts to many environmental stresses, including dehydration. It is composed of OsDREB2A and OsDREB2B, which convey the stress response via an ABA-independent route **Table. 3** [232]. Through their interactions with other transcription factors, including BR regulated [233], WRKY [234], MYB [235], and zinc finger transcription factors [236], several AP2/ERF transcription factors control plant growth and development as well as stress response. Transcription factor of WRKY, OsWRKY21 (LOC_Os01g60640) [237].

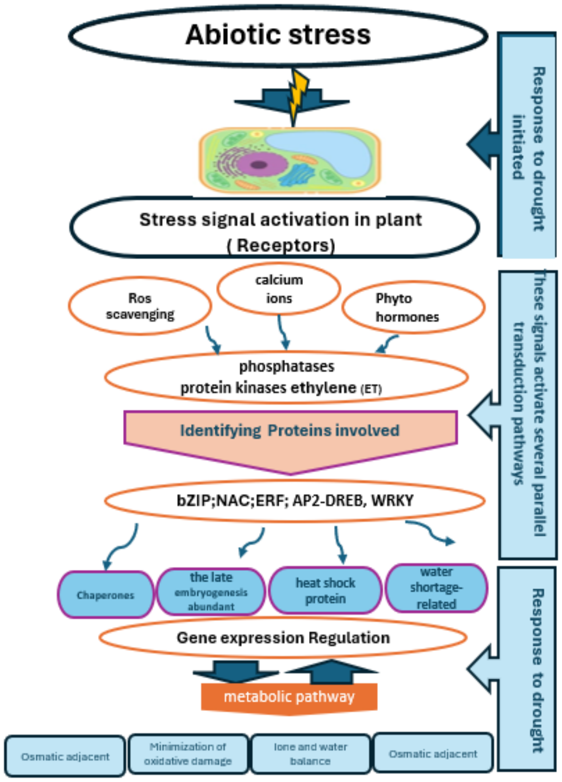

Figure 1. Model for transcription factors regulating abiotic stress-signaling pathways. (modified149).

In addition to increasing crop resilience to drought conditions by selecting drought-tolerant germplasms from a large pool of candidates, molecular breeding approaches, such as marker-assisted selection, might be utilized to produce distinct crop populations with increased drought tolerance [238]. Nevertheless, these molecular markers can be used to enhance the crop improvement process and to filter drought-tolerant germplasms from the vast pool of possibilities. The main methods for determining which genes in rice are in charge of drought resistance are DNA studies that make use of marker-based phenotyping. Despite significant progress in discovering drought-resistant characteristics, only a small number of these features have been identified so far [239,240]. Previous molecular genetic investigations have identified several QTLs linked to different physiological and biochemical parameters [241,242,243,244]. However, these investigations were unable to identify the genes responsible for these features because of low mapping specificity and a limited phenotypic effect [245,246]. In 1995, The International Rice Research Institute (IIRI) Philippines carried out the first QTL tagging for root-associated characteristics. Since then, several QTLs have been identified for features that are thought to help various crops withstand drought. Various morphological and physiological traits along with their corresponding QTLs are involved in mechanisms for drought adaptation and tolerance and have been reported in cereals. For example, Grain yield [247]; Osmotic adjustment [248]; Root traits [249]; Basal root thickness and 100-grain weight [250]; Plant production [250]; Filled grain number per panicle [75]; Panicle number per plant [75].

However, molecular breeding offers a chance to improve crop types, boost yield kinds, and generate safe harvests and agronomically sound, using markers for molecular screening is advantageous. Numerous QTLs linked to drought-resistant features have been tagged using various markers, including RFLPs, RAPDs, CAPS, PCR indels, AFLPs, microsatellites (SSRs), SNPs, etc. **Table. 3**. Numerous investigations have been conducted to identify qualitative trait loci (QTLs) associated with different qualities, according to [47,244,61].

Table 3. Application of DNA markers in horticultural crops for abiotic stress.

Crop	DNA Marker	Objective	Ref.
Miscanthus sinensis Perennial grass	SSR	To formulate SSR markers linked to drought resistance by utilizing transcriptome sequencing	[264]
Salvia miltiorrhiza Salvia	AFLP	- To segregate drought-related genes in sterile male and fertile near-isogenic lines of S. miltiorrhiza - To evaluate the change in fertility of plants during drought stres	[265]
Fragaria ananassa Duch. Strawberry	Expressed sequence tag (EST)	- To assess the correlation between leaf WLR and RWC and specific DNA markers	[266]
Manihot esculenta Cranz Cassava	Expressed sequence tags–simple sequence repeat (EST–SSR) markers	- Marker-assisted selection of progeny tolerance to drought stress - Identification of specific gene associations related to drought stress resistance	[267]
Glycine max Soybean	SSR (Satt226)	aims to identify and confirm quantitative trait loci (QTL) in Nepalese soybean, providing genetic markers for drought-tolerant varieties, enhancing food security, and improving resilience in water-limited environments.	[268]

Glycine max Soybean	SSR (Sat_044)	The study aims to identify quantitative trait loci (QTL) linked to soybean responses to water-deficit stress, aiding in understanding the genetic basis of drought tolerance, potentially improving productivity and stability.	[269]
Glycine max Soybean	SSR (Satt205-Satt489)	The study aims to identify quantitative trait loci (QTL) linked to soybean responses to water-deficit stress, aiding in understanding the genetic basis of drought tolerance, potentially improving productivity and stability.	[270]
Glycine max Soybean	RFLP (A489H)	A489H is associated with specific loci, these loci could include genes related to: **ABA Signaling Pathway**: Important in regulating drought stress responses. **Water Transport Genes**: E.g., aquaporins or genes controlling stomatal regulation. **Dehydration Response Proteins**: Such as late embryogenesis abundant (LEA) proteins.	[271]
Glycine max Soybean	RFLP (B031-1, A089-1, cr497-1, K375-1, A063-1)	The study aims to identify molecular markers in soybeans related to water use efficiency and leaf ash content, providing genetic markers for breeding programs to enhance water use efficiency and stress tolerance, promoting sustainable production.	[272]
Sesamum indicum Sesame	SNPs	The study uses genome-wide association studies (GWAS) and transcriptomic analyses to identify genes and pathways linked to drought resistance, aiding in breeding drought-tolerant sesame varieties for improved crop productivity. The study examines 400 accessions of sesame, focusing on genetic factors contributing to drought resistance, to enhance crop yield and stability, and potentially aid in drought-tolerant breeding programs.	[273]
Arachis hypogaea Groundnut	SSRs	The study aims to identify quantitative trait loci (QTLs) associated with drought tolerance traits in groundnut, a complex trait influenced by multiple genetic factors, providing a comprehensive genetic basis for breeding drought-tolerant groundnut varieties. .	[274]
Arachis hypogaea Groundnut	SSRs	The study aims to analyze quantitative trait loci (QTL) in cultivated groundnut (Arachis hypogaea) and create a consensus genetic map for drought tolerance traits, aiding breeding programs for drought-tolerant groundnut varieties.	[275]
Carthamus tinctorius L. Safflower	SSRs and ISSRs	The study aims to create a QTL linkage map for safflower, focusing on drought tolerance traits during reproductive stages, to enhance drought resilience and productivity in arid and semi-arid regions.	[276]
Gossypium hirsutum Cotton	Single strand conformation polymorphic (SSCP)	QTL identification associated with drought resistance in inbred lines with developmental resistance	[277]
Sorghum bicolor	Restriction fragment length polymorphism (RFLP)	Identification of lodging resistance and drought resistance prior to blooming	[278]
Triticum aestivum wheat	Simple sequence repeats (SSR), diversity array technology (DarT), gene-based marker for Vrn-A1	Genetic structure of drought tolerance by reproductive stage, formation of drought tolerance morphological approach concentrating on premature microspore stage of pollen formation for removing stress during flowering time	[279]
Triticum aestivum wheat	Simple sequence repeats (SSR)	To determine how SSR markers relate to chromosome 2A's drought resistance trait	[280]

In conformity with recent findings, numerous agronomic characteristics, such as resistance to drought, are considered quantitative, since they are controlled by multi-genes, also referred to as polygenes. As a result, the chromosomal loci that contain these kinds of genes are now known as quantitative trait loci (QTL). Direct selection under stressful conditions, whether natural or simulated, or identifying QTLs (polygenes) and then using marker-assisted selection are two ways to take use of a crop's inherent genetic variety [251].

For example, some SSR markers linked to these QTLs have also been discovered [252], for molecular screening may be used to quickly and accurately profile the rice lines by checking for drought tolerance in a new genotype of rice. (Barik et al, 2019) [244], looked at the genetic mapping of morpho-physiological variables linked to drought tolerance in rice throughout the reproductive stage. Under drought stress, they discovered five QTLs that control leaf rolling, leaf drying, harvest index, spikelet fertility, and relative water content, respectively: qLR9.1, qLD9.1, qHI9.1, qSF9.1, and qRWC9.1.

Recently, molecular tools have been utilized to accelerate crop yield improvement [253]. One such tool that has become prevalent in breeding programs is marker-assisted selection (MAS), which enhances breeding efficiency [254]. A variety of MAS strategies have been developed, such as marker-assisted backcrossing [255,256], which involves foreground and background selection [257,258]. Additionally, favorable alleles can be enriched in early generations [259,260], and selection for quantitative traits can be performed using markers at multiple loci [261,262]. Multiple cycles of selection can also be employed [263]. (Frisch and Melchinger, 2005) proposed a selection theory for marker-aided backcrossings, which suggests that the selection response depends on the marker linkage map and parents' marker genotypes[264].

Conclusions and Future Research Priorities

The acceleration of climate change poses a significant threat to global food security, with droughts severely impacting plant growth, development, productivity, and survival. Despite their vulnerability to water scarcity, plants have evolved various drought-resistant traits to mitigate the negative effects of stress. Under limited water conditions, plants activate internal defense mechanisms to minimize water loss. These responses begin with the perception of environmental signals and extend to physiological and metabolic adaptations governed by endogenous developmental programs, enabling plants to withstand adverse conditions such as drought.

The changes in physiology, metabolism, and morphology that protect plants from drought are considered key adaptations to drought. Different combinations of these traits lead to diverse strategies for coping with water scarcity. The morphological, physiological, and metabolic characteristics of plants can vary widely, as they coordinate their responses to environmental constraints in order to improve adaptation. Furthermore, varying levels of adaptability can coexist, enabling whole distinct biological models.

The present knowledge regarding drought stress genes was covered in this review, with particular attention paid to four popular plant responses to stress strategies which are physiological, morphological, sensing transduction, and molecular levels which have been the primary focus of these strategies for improving agricultural drought tolerance.

At the molecular level, TFs have been reviewed to show their roles in drought stress and their apparent connection to both ABA-dependent and -independent pathways. Significant advancements have been made in recent years in understanding the molecular processes that govern drought stress tolerance in plants. These advances have highlighted the role of molecular mechanisms in regulating the expression of genes involved in various adaptive processes. Such adaptations, manifested as morphological, physiological, and metabolic modifications, occur at both the cellular and organismal levels across different stages of plant development [281].

Despite these strides, progress in identifying the genetic determinants of drought resistance remains limited. The intricate nature of drought resistance, encompassing a wide range of interconnected physio-biochemical processes, poses significant challenges. In particular, comprehensive knowledge of the roles, interactions, and regulatory networks of these genetic factors is still lacking.

To fully harness the potential of transcription factor (TF) manipulation for improving drought resistance, several key challenges must be addressed. These include deciphering the complex gene regulatory networks that mediate drought responses, identifying stress-responsive TFs with high precision, and understanding how these factors interact within broader signaling pathways. Addressing these gaps is essential to enable the effective application of genetic engineering and breeding strategies aimed at enhancing crop resilience to drought stress.

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In addition, molecular genetics provides numerous DNA markers that explore genetic modification, genotypic resistance, stress-tolerant lines, and genetic information related to abiotic stresses. Early molecular marker technology provided DNA markers that offered basic information about stress resistance [149].

However, current advanced marker applications can now identify specific genes or groups of genes responsible for abiotic stress tolerance. Combining DNA markers with QTL mapping illustrates a pattern of stress tolerance genes on specific chromosomal loci. However, the demand for continuous improvement in DNA marker technology will allow even more detailed analysis of stress tolerance as climate changes.

In natural environments, plants are often subjected to multiple abiotic stresses simultaneously. To survive these conditions, numerous genes and distinct stress response pathways are co-activated, which may interact in either antagonistic or synergistic ways. The complexity of these interactions can be further amplified by the overexpression of specific transcription factors (TFs), potentially influencing other signaling pathways due to the intricate regulatory networks connecting various TFs across multiple levels.

Developing stress-resistant crop varieties through the manipulation of regulatory genes requires a thorough understanding of regulatory networks and the functional roles of transcription factors (TFs). Emphasizing the identification and characterization of stress-responsive TF genes should remain a primary focus of research in this field [149].

Conflict of interest

The author declares no conflicts of interest

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