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FROM SIPPING TO SURVIVING: ELUCIDATING THE INTRICATE MOLECULAR PATHWAYS GOVERNING DROUGHT TOLERANCE IN PLANTS

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ABSTRACT

Both the productivity of the world's agriculture and the stability of the environment are seriously threatened by drought stress. In order to survive and adapt to scenarios of inadequate water supply, plants have developed a variety of strategies. To improve crop resilience and water usage efficiency, it is crucial to understand the underlying processes of drought resistance in plants. The main processes that allow plants to endure drought stress will be briefly discussed in this review article. To maximise water intake and prevent water loss, plants first adopt a variety of morphological adaptations, such as the formation of deeper root systems, greater root hair density, and decreased leaf area. By making modifications, the plants are able to absorb water better and utilize the available water more efficiently. Second, during drought, plants use physiological responses to control water loss and keep their cells hydrated. Stomata, which are tiny apertures on the surface of the leaf, are closed as part of this process to stop transpiration and save water. Proline, sugars, and organic acids are examples of osmo-protectants that plants may produce. These substances function as compatible solutes to preserve cellular water potential and save important cellular structures.

Additionally, plants activate genes that encode proteins engaged in numerous processes that respond to drought at the molecular level. The production and control of stress hormones including abscisic acid (ABA), which is essential for stomatal closure and stress signalling, are carried out by these proteins. In addition, plants turn on their antioxidant defence mechanisms to scavenge reactive oxygen species (ROS) produced during dry conditions, reducing oxidative damage. As a result, plants have developed a sophisticated network of defences to adapt to and live-in drought-like environments. For the purpose of improving crop drought resilience and reducing the detrimental effects of water scarcity on ecosystems and global food security, it is essential to understand these mechanisms. The complex interactions among genetic, physiological, and environmental elements that affect a plant's ability to withstand drought in the future should be the main focus of study in order to develop water-limited areas' sustainable farming practises.

Keywords: Drought resistance; Plant physiology; Molecular mechanisms; Stress signalling; Adaptation strategies.

Introduction

Numerous stressors, including drought, salinity, heat stress, low temperature, heavy metal toxicity, flooding, and fluctuations in soil pH, are routinely presented to plants. Additionally, biotic elements like diseases, insects, etc. present difficulties for plants. These abiotic and biotic variables restrict the development and productivity of plants. For these factors to have a significant impact on the performance and physiology of individual plants or populations, they must go beyond the normal range of environmental variation (Farooq *et al.*, 2009).

Drought is a term used in meteorology to describe a prolonged period without significant rainfall. When this happens, the available soil-water becomes limited, and atmospheric conditions lead to continuous water loss through transpiration or evaporation. This can cause drought stress, which is a major abiotic stressor that has adverse effects on crop growth and yield. These modifications are mostly linked to changed metabolic processes, such as reduced or absent photosynthetic pigment production, ion uptake and translocation, glucose biosynthesis, food metabolism, and growth promoter synthesis. These modifications to metabolic processes and photosynthetic pigment synthesis have a direct impact on how much biomass a plant produces (Jaleel *et al.*, 2009). Drought stress is the most common environmental factor that limits crop productivity, and its severity is increasing due to global climate change (Khan *et al.*, 2013). Drought can also impair plant respiration, photosynthesis, and stomatal movement, which can have an impact on plant development and physiological metabolism. Drought is one of the major constraints on plant growth. Plants activate their drought response mechanisms in response to drought stress, including morphological and structural changes, expression of drought-resistant genes, synthesis of hormones, and production of osmotic regulating chemicals (Escalona *et al.*, 2000).

For the food security of the expanding world population, crop output must be increased and yield stability must be maintained under both normal and drought stress situations. It is challenging to determine how different DR components contribute to the stability of agricultural yield as the primary goal (Basu *et al.*, 2016). However, natural populations have a wide range of mechanisms for drought escape, avoidance, or tolerance that can enhance DR and keep crop plants' grain yields stable. The term "drought resistance" (DR) is more general and refers to plant species with coping mechanisms that allow them to resist, avoid, or survive drought stress (Bohnert *et al.*, 1995; Rizhsky *et al.*, 2002). The capacity of a plant species to finish its life cycle before the start of drought is known as "drought escape." Because of their ability to adjust their vegetative and reproductive growth in response to water availability, plants do not experience drought stress. This is primarily due to two separate mechanisms: fast phenological development and developmental flexibility. Rapid phenological development is characterised by rapid plant growth, which results in the production of a small number of seeds before the soil water supply runs out. These plants are thought to lack any unique morphological, physiological, or biochemical adaptations (Jones *et al.*, 1981; Mittler *et al.*, 2006).

Plants have developed a variety of adaptations to deal with drought. Drought avoidance and drought tolerance are the two main strategies that these adaptations fall under. In the dry season, plants having mechanisms for developmental flexibility grow slowly and produce few flowers and seeds, but in the wet season, they grow indefinitely and produce a lot of seed. "Drought avoidance" refers to the plant's ability to retain relatively higher water content in its tissues despite a decrease in water content in the soil (Basu *et al.*, 2016; Verslues *et al.*, 2011). The minimization of water loss (water savers) and optimisation of water uptake (water spenders) are two adaptive features that help achieve this. Water spenders maintain water absorption under drought stress by increasing roots, hydraulic conductivity, etc. Water spenders attain higher tissue water status in this way (Hasegawa *et al.*, 2000). While under drought stress, water savers make more efficient use of water by lowering transpiration, transpiration area, radiation absorption, etc. To stop water loss, some of these techniques include decreasing leaf area, deepening roots, and sealing stomata. Plants' capacity to withstand low tissue water content is known as "drought tolerance" (DT). These adaptive characteristics include enhancing protoplasmic resistance and maintaining cell turgor through osmotic adjustment and cellular flexibility. While there is less water available, plants can still grow and function because of drought tolerance strategies. These tactics include the build-up of osmotically suitable solutes, such as sugars and amino acids, which support cellular osmotic stability and guard against dehydration-related harm (Morgan *et al.*, 1984; Cramer *et al.*, 2011).

In this phase of climate change, to ensure food security, as well as sustainability, plant breeders and geneticists, are attempting to develop crops with greater drought resistance. In order to do this, crop breeding programmes must discover the genes and traits linked to drought tolerance.Researchers are also investigating the possibilities of biotechnology and genetic engineering to improve drought resistance in plants. For instance, researchers are looking into the field of genetic engineering to develop genes that code for transcription factors that are responsive to drought, osmotic adjustment enzymes, and proteins that control water transport and storage (Kiani *et al.*, 2008; Rizhsky *et al.*, 2002). Overall, drought resistance in plants is a complex trait that involves multiple mechanisms and pathways. Understanding these mechanisms and developing new strategies to enhance drought resistance in crops is essential to ensure global food security and sustainability in the face of climate change.

Mechanisms of drought tolerance

(A) Morphological mechanisms

Plants that are stressed by drought will first react by altering their exterior form and internal structure. The plant grows slowly and may possibly die as a result of water loss, which is the most severe consequence. According to studies, plants under abiotic stress can change their phenotypes to adapt to their environment. As a result, xerophytes have developed specific morphological traits as a result of environmental influences, and under these traits, they have adapted to drought in their ontogenetic development. In terms of leaves, stems, roots, and other plant parts, drought-resistant plants have some morphological as well as structural traits that were suited to the arid climate (Yang *et al*., 2021).

Here are some examples of morphological mechanisms of drought tolerance in plants:

1. Root architecture: Plants can adapt to water stress by changing their root architecture to improve water uptake. Drought-tolerant plants tend to have deeper, more extensive root systems that can access water from deeper soil layers. Some plant species also develop roots with a greater surface area to enhance water absorption. (Lynch, 2013)
2. Leaf morphology: Plants can also modify their leaf morphology to reduce water loss and increase water-use efficiency. Drought-tolerant plants often have smaller leaves with a lower surface area to volume ratio, which helps to reduce transpiration rates. Some plants also have specialized leaf structures, such as succulent leaves, that can store water for later use. (Chaves *et al*., 2002)
3. Stem morphology: Plants can also modify their stem morphology to enhance water storage and transport. Drought-tolerant plants often have thicker stems that can store water, as well as specialized tissues for water transport, such as xylem and phloem. Some plants also have the ability to shed their leaves or reduce their leaf area in response to water stress, which helps to conserve water. (Ehleringer& Dawson, 1992)
4. Trichomes: Trichomes are hair-like structures found on the surface of leaves and stems of plants that can help to reduce water loss by reflecting sunlight, increasing the boundary layer around the plant surface, and physically blocking transpiration. Drought-tolerant plants often have more trichomes, which can reduce water loss by up to 50%. (Samarah *et al*., 2004)

When exposed to drought, plants undergo a variety of changes, including those that affect the entire plant, individual tissues, and the physiological and molecular levels of the plant. Under dry conditions, plants use a variety of morphological strategies, including:

a. **Drought escape:** Some plants use mechanisms that abbreviate their life cycles through rapid development, seasonal growth, and self-reproduction before the start of the dry season in order to avoid the damaging effects of drought stress on plant health and productivity (Álvarez *et al*., 2018). Early flowering is arguably the best escape adaptation mechanism that plants can have (Tekle & Alemu, 2002). Before the plant's life cycle was terminated by the drought, escape from it allowed for the creation of fresh seeds. Plants grow more quickly and show lower vegetative growth under these circumstances. Short life cycles are therefore thought to be a suitable strategy for escaping from climate pressures. However, this mechanism may result in a significant shortening of the plant's growing season, which may compromise plant output in some circumstances (Araus *et al*., 2002).

b. **Avoidance:** Drought avoidance, also known as dehydration avoidance in previous studies, depends on reducing plant water loss by controlling transpiration and improving water use efficiency. The root system also plays a crucial part in preventing drought mechanisms, and as it gets thicker and deeper, it can absorb water from deeper levels, which helps plants produce more yield when there is a drought. Plants that are in this condition reduce transpiration, restrict vegetative growth, or increase root growth to store water and prevent dehydration during brief drought stress periods (Dobra *et al*., 2010). High plant water potential is maintained in the avoidance approach by decreased transpiration loss and higher water uptake by developed root systems. In some circumstances, xeromorphic traits such cuticles and the presence of hairy structure on leaves do contribute to the maintenance of high-water potentials in plant tissues. Notably, excessive development of these structures may result in decreased output and smaller vegetative and reproductive portions (Boulard *et al*., 2017).

c. **Phenotypic flexibility:** In reaction to drought stress, plants lowered the number and size of leaves only to reduce water consumption and prevent yield loss, which is known as a morphological mechanism. Additionally, since the root system is the sole way for plants to take water from the soil, increasing root growth rate, root density, spread, and size are some of their primary responses to drought stress (Tzortzakis *et al.*, 2020). This is especially true for plants with small leaves (Dai, 2013). The ability of the plant to survive water shortages in arid situations is also demonstrated by the synthesis of trichrome on the leaves (Zhang *et al.*, 2019). The rate of light reflection increases in the leaf, lowering the leaf temperature, while trichomes add another layer of water-resistance, slowing the rate of water loss by transpiration (Tiwari *et al.*, 2021).

Overall, morphological mechanisms of drought tolerance in plants involve a range of physical adaptations that allow plants to survive and thrive under water stress conditions. By understanding these mechanisms, plant breeders and geneticists can develop crops with improved drought resistance and water-use efficiency.

(B) Physiological mechanisms

Physiological mechanisms of drought resistance in plants refer to the internal changes that occur in plants to help them cope with water stress conditions. These mechanisms involve alterations in the plant's physiological processes, such as changes in water use efficiency, photosynthesis, and hormone levels. Here is a table summarizing some key physiological responses and their contributions to drought tolerance in plants, along with relevant references.

Table 1: Physiological Responses and Contributions to Drought Tolerance in Plants: A Summary and Relevant References

Physiological Response	Contribution to Drought Tolerance	Reference
Stomatal Closure	Reduces water loss through transpiration by closing stomata, thus conserving water within the plant	Tardieu & Simonneau (1998)
Leaf Rolling	Minimizes leaf surface area exposed to the atmosphere, reducing water loss	Chaves *et al*., (2002)
Osmotic Adjustment	Accumulation of osmolytes (compatible solutes) in cells to maintain cellular water potential and prevent water loss	Blum A. (2017)
Abscisic Acid (ABA)	Hormone involved in stomatal closure, regulates drought-responsive gene expression, and triggers other adaptive responses	Cutler *et al*. (2010)
Root Architecture	Development of deep and extensive root systems to enhance water uptake from deeper soil layers	Lynch J. P. (2013)
Antioxidant Enzymes	Production of enzymes like superoxide dismutase (SOD) and catalase to scavenge reactive oxygen species (ROS) under drought stress	Mittler R. (2002)
Photosynthetic Adjustments	Regulation of photosynthetic processes to maintain energy balance under water-limited conditions	Flexas *et al*., 2016
Leaf Senescence	Premature leaf aging and shedding to prevent further water loss and reallocate resources towards essential plant parts	Lim *et al*., 2007

Here are some examples of physiological mechanisms of drought resistance in plants:

(a) Water use efficiency /Transpiration and stomatal conductance:

By minimising the quantity of water lost through transpiration, plants can improve the efficiency of their water consumption. To do this, the stomata, which are tiny holes on the surface of the leaf that control gas exchange, must be closed. Under water stress, drought-tolerant plants often use water more efficiently and sustain a greater rate of photosynthesis (Flexas *et al.*, 2016). Plants immediately seal their stomata in reaction to stress brought on by drought. It also has additional impacts including lowering the intake of nutrients and carbon dioxide, which in turn changes metabolic processes like photosynthesis. This helps to decrease water loss through transpiration. To further reduce transpiration while under drought stress, plants that thrive in arid environments have evolved xeromorphic characteristics (Xiong& Zhu, 2002). They may do this by employing techniques like leaf shedding (in deciduous species), as well as by reducing the quantity, size, and branching of their leaves. Another adaptation to combat drought stress is sclerophylly, where plants develop hard leaves that are less susceptible to wilting and can fully recover when normal conditions return (Aroca, 2012). Recent research has shown that the reduction in stomatal conductance during drought stress is related to anatomical traits that reduce the amount of chloroplast surface area exposed to the intercellular space per unit leaf area, in addition to the reduced expression of aquaporin genes, which are involved in water transport (Tosens *et al.*, 2012).

Drought stress interacts with a number of additional variables, such as the stage of leaf development and the amount of light available, to change the differentiation of mesophyll cells and chloroplasts, eventually reducing conductance and the capacity for photosynthesis (Fang *et al.*, 2015). Additionally, when subjected to drought, plants adjust by decreasing the size and quantity of stomata in order to live. In conclusion, plants close their stomata in response to drought stress, which lowers water loss but also impairs CO_2 and nutrient intake. To further reduce transpiration, plants in arid environments have developed a variety of techniques, including xeromorphic characteristics, leaf shedding, and sclerophyll (Iqbal *et al.*, 2013). Not only are physical adaptations to the drought responsible for the reduction in stomatal conductance, but also changes in gene expression. Other elements, such as the stage of leaf growth and the availability of light, also affect how plants react to drought stress. Plants can adapt to drought by lowering the size and quantity of their stomata (Wan *et al.*, 2009).

(b) Photosynthesis

Plant photosynthesis is negatively impacted by drought stress, which reduces growth and output. However, drought-tolerant plants may modify their photosynthetic apparatus to sustain a greater rate of photosynthesis under water stress. In order to deal with the scarce water supply, this entails boosting the activity of carbon fixation-related enzymes (Lawlor&Cornic, 2002). Crop productivity is heavily reliant on photosynthesis, which is negatively impacted by water shortages. Stomata close when plants are under moisture stress, which lowers the capacity of the leaves for photosynthetic activity. Chloroplasts become dehydrated as a result, and the diffusion of carbon dioxide into the leaf is reduced (Li *et al.*, 2013). The extent of the impact on photosynthesis depends on the severity of the drought and the developmental stage of the plant. Reduced leaf area and photosynthetic rate per unit leaf area are two effects of drought stress on photosynthesis. Stomatal closure or metabolic dysfunction are the main causes of the decrease in photosynthetic rate. Drought stress causes the photosynthesis processes to continue but with less carbon dioxide present, which results in the accumulation of diminished photosynthetic electron transport components. This accumulation can generate reactive oxygen species (ROS), which can cause significant damage to the photosynthetic apparatus (Chastain *et al.*, 2016).

In order to reduce damage to photosynthesis brought on by drought, plants have evolved adaptive mechanisms. The xanthophyll cycle, the water-water cycle, the dissociation of the light-harvesting complexes from the photosynthetic reaction centres, and thermal dissipation of light energy are some examples of these adaptations (Niyogi, 1999). Changes in the photosynthetic carbon metabolism are principally responsible for the metabolic deficit during drought stress. Hormones, ROS, carbohydrates, and other metabolic processes interact in a complicated way to help plants respond to drought stress (Demmig-Adams & Adams, 2006). In conclusion, the effects of drought stress on photosynthesis have an adverse effect on plant development and production. While under water stress, drought-tolerant plants use a variety of methods to sustain a greater photosynthetic rate. Adjustments to the photosynthetic system and the activation of defences against oxidative damage are two examples of adaptive reactions.

(c) Hormone regulation

The levels of plant hormones, including cytokinins and ABA, which are crucial for controlling plant growth and development, can also be affected by drought stress. To encourage root development and water absorption, drought-tolerant plants can maintain a balance between ABA and cytokinins (2010, Zhang & Davies). Major phytohormones including auxin, ethylene, gibberellic acid, cytokinin, abscisic acid, and others govern a variety of mechanisms that allow plants to adjust to drought stress (Wilkinson *et al.*, 2012). The primary hormone that is synthesised in roots and transported to leaves to begin drought stress adaptation in plants through stomatal closure and decreased plant development is called ABA (Wilkinson & Davies, 2010). Nevertheless, enhancing the ABA-induced drought adaptation in plants to maximize yield poses a significant challenge due to the potential unintended consequences of reduced carbon assimilation caused by stomatal closure and ABA-induced senescence, particularly when drought stress occurs during the reproductive stage. Several ABA signaling genes, including OsNAP, $OsNAC_5$, and DSM_2, have been identified as key regulators that can enhance yield under reproductive drought conditions (Liang *et al.*, 2014; Du *et al.*, 2010).

It has been discovered that the buildup of abscisic acid (ABA) during the expression of drought tolerance reduces the synthesis of ethylene, hence preventing ethylene-induced senescence and abscission. Sharp (2002) found that ABA-deficient maize seedlings produced more ethylene and were more susceptible to drought. On the other side, auxins have been found to be unfavourable regulators of drought tolerance. In wheat leaves, the ability to withstand drought stress was followed by a drop in the amount of indole-3-acetic acid (IAA) (Xie *et al.*, 2003). According to research by Zhang *et al.* (2009), IAA suppression encourages the accumulation of late embryogenesis-abundant (LEA) mRNA, which aids rice in adapting to drought stress.

On the other hand, when maize leaves were subjected to water stress, endogenous zeatin and gibberellin (GA_3) levels rapidly decreased, which was connected with higher cell damage and a reduction in plant growth. In response to lower production or increased degradation, plants under drought stress showed decreased cytokinin content and activity (Pospisilova *et al.*, 2000). Reduced cytokinin content brought on by drought increased senescence in lucerne (Goicoechea *et al.*, 1995). Senescence is known to be delayed by cytokinins, and higher levels of endogenous cytokinin caused by overexpression of the ipt gene, which is involved in cytokinin production, delayed drought-induced senescence and encouraged stress adaption (Peleg and Blumwald, 2011). Cytokinins are also negative regulators of root development and branching. Drought-induced root-specific cytokinin breakdown facilitated primary root growth and branching, which eventually improved Arabidopsis' ability to withstand drought (Werner *et al.*, 2010).

(d) Osmotic adjustment

Different strategies are used by drought-tolerant plants to adapt and resist water stress. The modification of cellular osmotic potential to maintain turgor pressure and avoid wilting is a significant adaptation. This is accomplished through the buildup of suitable solutes, such proline and glycine betaine, which shield plant cells from oxidative stress and dehydration (Chen & Murata, 2011). During times of drought, osmotic adjustment is essential for sustaining physiological activity and cell turgor. When compared to tolerant genotypes, sensitive plant genotypes are more impacted by decreased relative water content in tissues (Upreti *et al.*, 2000). By lowering the osmotic potential and consequently preserving turgor and reducing leaf water volume, the accumulation of solutes is essential for drawing water into the cell. By actively collecting solutes in the cytoplasm, osmotic adjustment helps balance cell water, reducing the detrimental effects of dryness on plant development. It prevents dehydration damage by maintaining physiological functions and cell turgor. Osmotic adjustment also speeds up the partitioning of pre-anthesis carbohydrates during grain filling, which aids in plant development in general (Morgan, 1990).

Osmotic adjustment involves the accumulation of solutes in dividing cells when water potential is reduced, aiding in maintaining turgor and enabling cell enlargement and growth. Osmotic adjustment is related to the preservation of stomatal conductance, photosynthesis, leaf water volume, and general development under drought stress conditions. It aids plants in adjusting to related changes such increased salt concentration and mechanical impedance as well as the decrease in water content (Chaves& Oliveira, 2004). The main solutes that build up in response to water stress are inorganic cations, organic acids, carbohydrates, and free amino acids. Along with osmotic regulation, compatible solutes like proline and glycine betaine also have a role in the detoxification of reactive oxygen species (ROS), maintaining the integrity of membranes, and stabilising enzymes or proteins. Osmotic adjustment is mostly regulated by enzymes like ornithine -aminotransferase (OAT), pyrroline-5-carboxylate reductase (P5CR), and betaine aldehyde dehydrogenase (BADH) (Ashraf & Foolad, 2007). They help the plant endure drought stress and make it easier for suitable solutes to accumulate. Therefore, osmotic adjustment is a key tactic used by plants to retain water and sustain increased cellular turgor potential while under moisture stress. The osmotic adjustment of leaves and drought tolerance have been found to be substantially associated in a number of crop species (Serraj & Sinclair, 2002). Plants modify their osmotic potential under water stress situations by raising the concentration of compatible solutes in the cytosol, which lowers the osmotic potential of cells and maintains turgor pressure and growth. During drought stress, proline is a frequent compatible solute that plants collect, albeit the amount accumulated varies depending on the cultivar and development stage (Oosterhuis & Wullschleger, 1987). In general, osmotic adjustment through the build-up of suitable solutes is a critical adaptation for plants to endure drought stress, keep their turgor, and ensure their survival and development in difficult water circumstances.

(C) Biochemical mechanisms of drought tolerance

Plants avoid a range of external stresses through morphological adaptation. The mechanism of drought tolerance is linked to several biochemical, morpho-physiological, and molecular processes (Cattivelli *et al.*, 2008). Among them, the most important mechanisms involve production of stress proteins and ROS scavenging system, which are explained below.

(a) Stress proteins/Drought-Induced Proteins: Plants create proteins in reaction to stress in order to live under various pressures, including drought.

Drought-induced proteins, which have a protective function in plant response to stress and can increase plant drought tolerance, are newly synthesised proteins in plants under drought stress. Since most stress proteins are water soluble, they serve a crucial role in stress tolerance by hydrating cellular structure (Wahid *et al.*, 2007). According to their roles, drought-induced proteins may be separated into two categories: (1) Ion channel proteins, LEA proteins, OSM proteins, and metabolic enzymes are among the functional proteins that directly protect cells. (2) Protein kinases, phospholipases C and D, calmodulin, G proteins, transcription factors, and certain signalling proteins are examples of regulatory proteins that are engaged in signal transduction or gene expression regulation in water stress and have indirect protective effects (Yang *et al.*, 2021). The following highlights three crucial drought-inducible proteins: LEA, AQP, and dehydrin.

i. Late Embryogenesis Abundant Protein

The Late Embryogenesis Abundant (LEA) protein is a protective protein that is enriched during the late stages of seed embryo development. Its expression is controlled by the stage of plant growth, ABA, indications of dryness, and other elements. Plants' tissues and organs include the LEA protein, which has a high degree of hydrophilicity and heat stability. Plants' tolerance for dehydration and tissues' defence against water stress are both directly correlated with LEA proteins' capacity to hold water inside cells. Even though the majority of LEA proteins lack a stable secondary structure, drying can cause them to take on α-helical form. Because of this structural modification, LEA proteins can now be extremely important in the defence against environmental stress (Bremer *et al.*, 2017).

Crop resilience to environmental stress is aided by LEA proteins, and the structure and makeup of these proteins' amino acids have a direct impact on how well they function. These proteins are particularly hydrophilic because they frequently include a high concentration of polar amino acids. Additionally, they show conserved sequences that, under stress, may fold into highly folded α-helical structures. Denatured proteins and membrane systems can interact with such structures to stabilise lipid membranes or functional proteins and reduce excessive water loss (Close, 2010). As a result, the effect of the external environment on intracellular metabolism is diminished. In addition, when LEA proteins are in dissolved state, they maintain a dynamic balance between random conformation and α-helical structure. Their participation in crop resilience to environmental stress is further facilitated by this characteristic. The capacity of LEA proteins to scavenge reactive oxygen species (ROS) in response to stress, such as drought, is a crucial function. Under unfavourable circumstances, plants produce a large amount of reactive oxygen free radicals, which have potent oxidative characteristics and can harm proteins and cell membranes. Therefore, in adverse conditions, scavenging reactive oxygen free radicals acts as a key defence mechanism for plants (Soulages *et al.*, 2003; Hara *et al.*, 2004). Overall, the LEA protein functions as a protective factor in plants, aiding in water retention, structural stability, and ROS scavenging, all of which help plants endure environmental stress.

ii. Dehydrin

Dehydrin, a member of the Lea-II protein family, is a drought-induced protein widely found in higher plants. It has a molecular weight ranging from 9 to 200 kDa. Dehydrin is produced during the late stages of embryogenesis and is largely accumulated in plants that are dehydrated as a result of drought, salt stress, and extracellular freezing. It also reacts to low temperatures and exogenous ABA. Dehydrin has a high hydrophilicity and is rich in glycine and lysine while being deficient in cysteine and tryptophan. Additionally, it is a heat-stable protein that holds up well in boiling water. It is thought that dehydrin is essential for defending cells against the harm brought on by dehydration (Allagulova *et al.*, 2003).

Dehydrin helps to keep the membrane system stable. Plant cells dehydrate while under stress, which interferes with the hydration defence mechanism on the surface of membrane lipid bilayers. As a result, the distance between lipid bilayers is reduced, membranes fuse, and the structure of the membrane is severely harmed. Dehydrin has a high capacity for hydration, which allows it to attach to membrane lipids and stop cells from losing too much water. This prevents a reduction in lipid bilayer spacing, which in turn inhibits membrane fusion and the breakdown of membrane integrity (Close, 2010). It also aids in maintaining the hydration protection system of membrane structure. Dehydrin also protects proteins by doing so. Dehydrin's K fragment acts as a molecular chaperone by forming an amphipathic -helix with the hydrophobic regions of partly denatured proteins. The action of the chaperones stops further protein denaturation. Numerous polar amino acid residues can interact synergistically with tiny polar molecules and low molecular weight substances (such as carbohydrates, amino acids, and water molecules) located in the nuclear matrix and cytoplasmic matrix because they are present in the core component of dehydrin. Dehydrin's ability to protect proteins is enhanced by this interaction (Alsheikh, 2003).

iii. Aquaporin

With a size range of 26 kD to 30 kD, aquaporins (AQP) are a type of intrinsic proteins found in the plasma membrane or vacuolar membrane that exclusively transport water. They are members of the same major intrinsic protein (MIP) protein family as ion channels and glycerol channels. The root epidermis, outer cortex, and endodermis cells, xylem parenchyma cells close to xylem arteries, phloem related cells, guard cells, and other tissues and organs that require a lot of water movement are just a few examples of where AQP is abundantly expressed (Yang *et al.*, 2021).

In water transportation, AQP is crucial. By lowering the resistance to transmembrane water transport and accelerating the rate of water migration along the gradient of water potential, AQP promotes the transmembrane transport of water inside and outside of cells during the transmembrane transport of water in plants. The water potential balance between xylem parenchyma cells and transpiration flow can also be maintained by plant AQP (Netting, 2000). Water is stored in the vacuole by AQP transport when the transpiration and water potential of the ducts are higher than those of parenchyma cells. AQP will transport the stored water to the ducts when the water potential of parenchyma cells is greater than the transpiration water potential of the ducts. via AQP, water is carried via the vacuole and plasma membranes of parenchyma cells. Aquaporin transports neutral small molecules that are crucial to many physiological processes in plants, including photosynthesis, nutrient uptake, cell signalling, and stress response, in addition to water molecules. These neutral small molecules include CO_2, H_2O_2, glycerol, NH_3/NH_4^+, boron, silicon, and urea. The role that AQP plays in alleviating drought stress depends on its function (Wudick *et al.*, 2010).

a. Reactive oxygen species (ROS)

Oxygen is essential for the survival of aerobic organisms as it supports various life processes. However, when oxygen is not completely reduced during metabolic reactions, it can give rise to a group of highly reactive chemical substances known as reactive oxygen species (ROS). ROS includes the superoxide radical O_2^-, hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), hydroxyl radical (·OH), and organic oxygen radicals (RO·, ROO·), among others (Mignolet-Spruyt *et al.*, 2016).

Under normal conditions, plants maintain a balance between ROS production and their scavenging system. However, when plants experience drought stress, this balance is disrupted. Drought conditions can lead to an increase in the production of reactive oxygen free radicals, resulting in oxidative stress within plant cells. If the production of ROS exceeds the capacity of the plant's ROS scavenging system, it leads to the accumulation of ROS and oxidative damage (Pospíail, 2012). The excessive production of these free radicals can have detrimental effects on cells, such as lipid peroxidation of cellular membranes, denaturation of proteins, DNA strand breakage, and impaired photosynthesis. To counteract the detrimental effects of reactive oxygen species (ROS), plants have developed an intricate network of enzymes and non-enzymatic antioxidants collectively known as the Reactive Oxygen Scavenging System. This system plays a crucial role in maintaining a delicate balance between ROS production and elimination, thereby preventing oxidative damage (Zia *et al.*, 2021).

Plants possess an antioxidant defense system comprising both enzymatic and non-enzymatic components. The enzymatic antioxidants include superoxide dismutase, polyphenol oxidase, peroxidase, ascorbate peroxidase, catalase, and glutathione reductase. Non-enzymatic antioxidants consist of β-carotene, ascorbate, α-tocopherol, glutathione, and carotenoids. These antioxidants work collaboratively to shield plants from the harmful effects of ROS (Zhu *et al.*, 2009; You and Chan, 2015).During drought stress, the significance of both enzymatic and non-enzymatic antioxidants becomes pronounced, as plants require higher concentrations of these antioxidants to mitigate the detrimental effects caused by drought. Enzymatic antioxidants exhibit remarkable efficiency in scavenging ROS, which is why many studies on drought tolerance report an upregulation of these enzymes (Farooq *et al.*, 2008). Various enzymatic antioxidants are involved in the scavenging of ROS within the glutathione cycle in the cell cytosol and stroma of different organelles. They demonstrate a correlation with drought tolerance in plants (Anjum *et al.*, 2011).

In addition to the traditional antioxidants, evidence suggests that soluble sugars, such as disaccharides, raffinose, and fructans, play a dual role in relation to ROS. Moreover, other mechanisms, including leaf movement and curling, as well as rearrangement of the photosynthetic apparatus, may represent the plant's efforts to balance the energy absorbed with the availability of CO_2, thereby preventing an over-reduction of ROS (Mittler, 2002). Overall, the Reactive Oxygen Scavenging System in plants encompasses a range of enzymatic and non-enzymatic antioxidants that work synergistically to combat ROS and safeguard plants against oxidative damage.

Plant response at gene level

At the gene level, plants exhibit various responses to drought stress. Drought triggers a cascade of molecular events that lead to changes in gene expression and the activation of specific pathways involved in stress tolerance and survival. Plants respond to stress by changing the expression of certain genes during drought conditions. At the transcriptional level, many genes are stimulated, and the gene products of these genes play a significant role in drought resistance (Kavar *et al*., 2008). However, it is widely known that drought tolerance is a complicated mechanism involving the intensive action of several genes. Gene expression may be directly induced by stress circumstances or damage reactions (Sharp *et al*., 1994; Agarwal *et al*., 2006).

In order to encourage the repair of damaged deoxyribonucleic acid, there is signalling for drought detection in plants as fast responses to stress via the redox system. Chemical signals like as reactive oxygen species, calcium, calcium regulated proteins (Joyce *et al*., 2003), mitogen-activated protein kinase cascades, and cross-talk between multiple transcription factors are among the many signalling mechanisms that play a significant part in signal transmission. It establishes a link between the perception of outside stimuli and cellular reactions (Wrzaczek&Hirt, 2001).

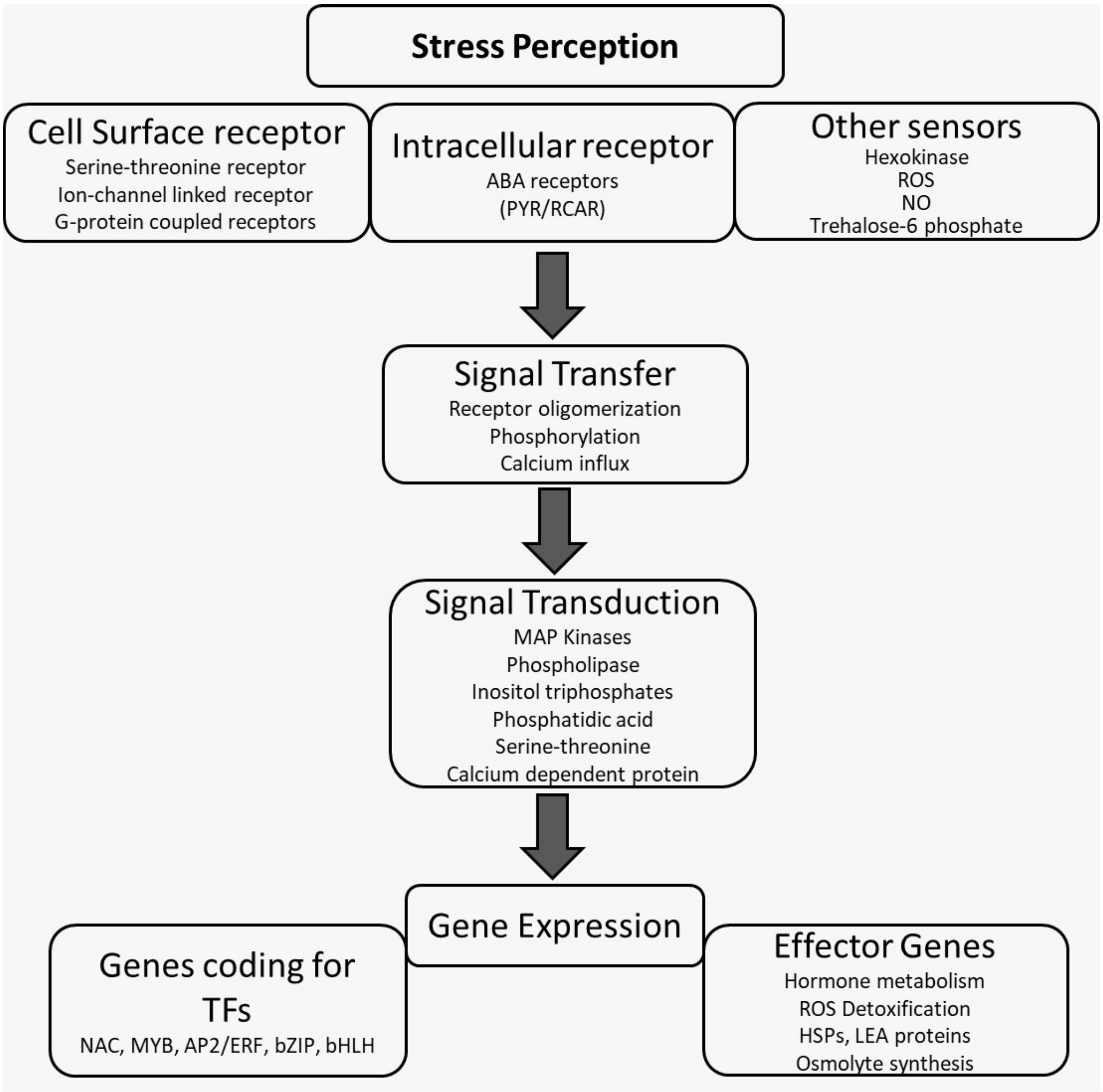

Fig. 1: Signalling cascade from perception of the drought signal to the regulation of gene expression

Here is a simplified explanation of the steps involved in the mechanism of plant response at the gene level in drought:

1. Stress perception

For plants to detect and react to drought stress, complex molecular systems have been devised. These strategies, which entail altered gene expression and signalling pathways, enable the plant to endure the stress and adapt to its surroundings (Zhu, 2016). The abscisic acid (ABA) pathway is one of the important signalling mechanisms involved in the sense of drought stress. A hormone called ABA is produced in response to the stress of drought and controls a number of physiological processes, such as stomatal closure, osmotic adjustment, and changes in gene expression (Hirayama & Shinozaki, 2010). The plasma membrane-based ABA receptors detect ABA and set off subsequent signalling processes that eventually activate genes that respond to stress. Previous studies reported that the intracellular receptor for ABA, PYR/RCAR activated the serine/threonine kinase SnRK2, which further showed signal for drought stress in response to ABA binding (Sheard and Zheng 2009). The ABA receptor can therefore be thought of as a stress sensor because it is known that stress can promote ABA production.

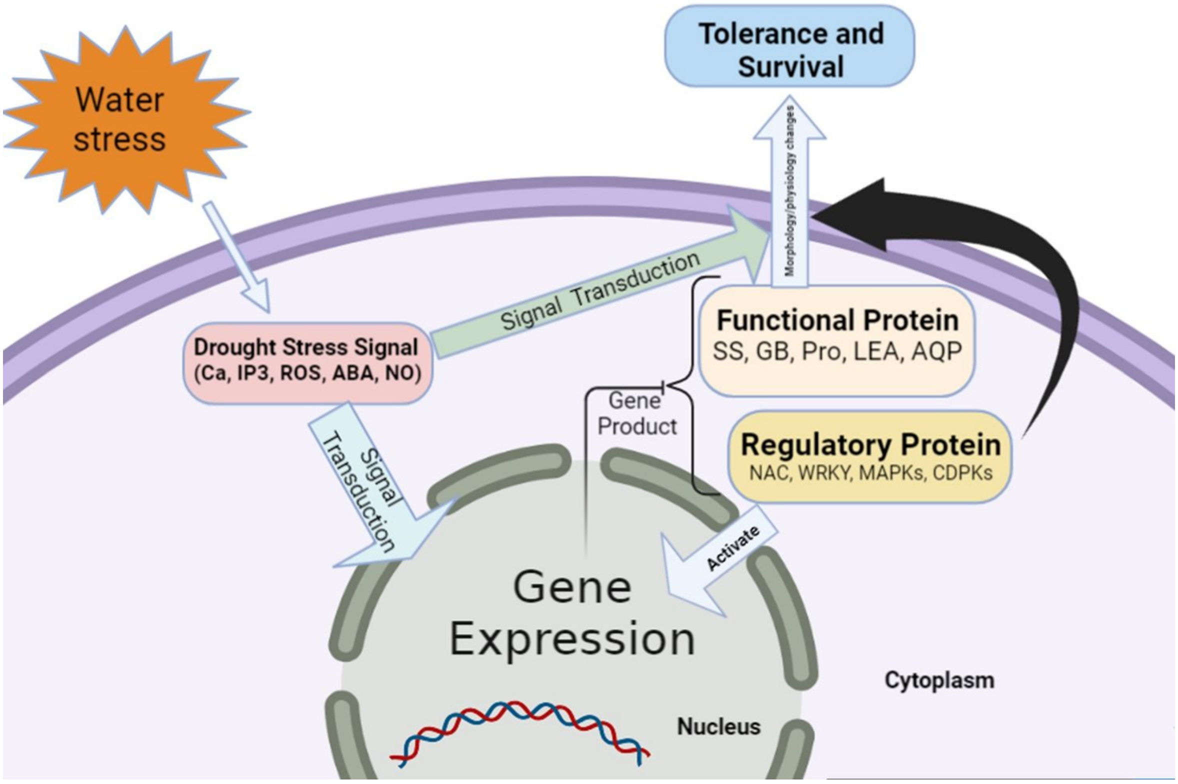

Fig. 2: The process of plant drought-tolerance development.

Additionally, drought stress can cause plant cells to produce ROS, which function as signalling molecules and cause a variety of stress response pathways to be activated. ROS can influence cellular metabolism and alter gene expression by activating transcription factors and MAPKs. Furthermore, the redox state of the ascorbate/dehydroascorbate and reduced glutathione/oxidized glutathione couples are anticipated to play a role in redox signalling because of the short half-life of ROS ((Yang *et al.*, 2021; Foyer &Noctor, 2000).

Besides, the modulation of ion channels and transporters is crucial for stress perception in plants. Drought stress alters the activity of ion channels and transporters involved in the movement of water and solutes across cell membranes. These changes in ion fluxes and transport help plants sense and respond to the water deficit conditions (Hadiarto& Tran, 2011).

Furthermore, transcription factors and gene regulatory networks are activated in response to drought stress, leading to the expression of stress-responsive genes. These genes encode proteins that play key roles in drought tolerance and adaptation, including enzymes involved in osmotic adjustment, detoxification of ROS, and synthesis of protective compounds. For instance, by changing the DNA methylation patterns of their promoters, the stress caused by a drought might cause the production of genes involved in osmotic adjustment (Singh& Laxmi, 2015). In conclusion, signalling pathways, changes in gene expression, control of ROS, and epigenetic alterations are all part of the complex and linked molecular mechanisms that contribute to plants' awareness of drought stress. Together, these processes allow plants to recognise drought stress, adapt to it, and eventually endure in harsh climatic conditions.

2. Intracellular Transduction Pathways and Regulation Mechanisms

The signal perception process is followed by the production of secondary signalling molecules, which are crucial for signal transduction. These molecules include protein kinases and phosphatases (serine/threonine phosphatases), phospholipids like phosphoinositides, ROS, Ca^{2+}, nitric oxide, cAMP, and sugars. These secondary messengers are essential for signal transduction, and they may act as common signal transducers for cross-talk between various stress-response pathways (Bartels & Sunkar, 2005; Tuteja & Sopory, 2008).

One of the primary methods for signal transduction is mitogen-activated protein kinases (MAPKs). Protein kinases called MAPKs are triggered by a variety of stressors, including drought stress. Downstream transcription factors that control the expression of stress-responsive genes can be activated by MAPKs. They cause protein phosphorylation and form a signalling cascade that connects the plasma membrane's stress sensor to the nucleus' control of gene expression. Through phosphorylation, transcription factors are activated as a result of MAPKs' nuclear translocation. Furthermore, MAPKs have the ability to control cellular functions as ion transport, ROS metabolism, and cell death (Tena *et al.*, 2001).

Additionally, stress causes a temporary rise in the amount of calcium in the cytoplasm, and this extra calcium comes from either cellular reserves or the apoplast. Cells have been shown to have a number of Ca^{2+} sensors, such as calmodulin (CaM) or CaM-binding proteins, which transmit the stress signal to the nucleus via other messengers like phospholipase D or Ca^{2+}-dependent protein kinases (Tuteja & Sopory, 2008). Besides, plasma membranes include phospholipids like phosphoinositides, which are the source of a number of secondary signalling molecules such phosphatidylinositol phosphates. Kinases (like PI3Kase) phosphorylate these molecules. These phospholipids are subjected to phospholipase action to produce signalling molecules such inositol 1,4,5-trisphosphate (IP3), diacylglycerol (DAG), and phosphatidic acid (PA), which are involved in intracellular signalling and the transmission of signals across the plasma membrane (Drobak& Watkins, 2000).

3. Signal transduction and response of acceptor cell

From sensing environmental stimuli to responding to them, plants typically use a three-part signal transduction process: (1) the sensory transduction and response of sensory cells to environmental stimuli, specifically the initial signal sensory transduction process, producing intercellular messenger; (2) the intercellular messenger is transmitted between cells or tissues, and ultimately acts on the receptor cell site; and (3) the transduction and response of acceptor cell. Intercellular messengers created during signal transduction cause particular reactions in acceptor cells when they come into contact with them (Davies & Zhang, 1991). The type of the signalling molecules and the particular receptors present in the acceptor cells can have an impact on the responses. Several typical reactions of acceptor cells to intercellular messengers are listed below:

Activation of intracellular signaling pathways: Intracellular signalling pathways are initiated when the intercellular messenger binds to its unique receptor on the acceptor cell. Protein kinases, intracellular calcium levels, or cyclic nucleotide concentrations can all change as a result of this activation. The signal is sent from the receptor through these signalling channels to cellular elements downstream (Nair *et al.*, 2019).

Gene expression and protein synthesis: Gene expression varies as a result of intracellular signalling pathways being activated. Specific genes are transcribed when transcription factors, which are triggered by the signalling molecules, bind to particular DNA sequences in the nucleus of the acceptor cells. A variety of cellular reactions, including the activation of enzymes, reorganisation of the cytoskeleton, or modifications to membrane characteristics, can be mediated by the newly synthesised proteins (Lodish *et al*, 2000).

Modulation of cellular processes*:* In acceptor cells, the intercellular messengers have the ability to control a variety of cellular functions. They may have an impact on organelle function, membrane transport, cell growth and division, and metabolism. For instance, the signalling molecules may impact cell cycle development, activate or inhibit enzymes involved in metabolic processes, or control ion channels for the movement of certain ions across the cell membrane (Nelson *et al.*, 2017; Lodish *et al*, 2000).

Changes in cell behavior and function: Acceptor cells' reactions to intercellular messengers can alter how they behave and perform. Changes in cell shape, migration, or differentiation are a few examples of these modifications. Acceptor cells may alter their form, migrate towards or away from certain stimuli, or undergo cell type specialisation in response to signalling molecules (Nair *et al.*, 2019).

Modulation of physiological responses: The physiological effects of acceptor cells' reactions to intercellular messengers can be more extensive. They may have an impact on how tissues and organs work, leading to coordinated reactions at the level of the entire organism. For instance, signalling molecules can control how stomata open or close in plants, how smooth muscles contract or relax in animals, or how hormones are secreted and how they are communicated (Guyton *et al.*, 2015; Hall, 2015).

Overall, acceptor cells' reactions to intercellular messengers are quite specialised and can result in a wide range of cellular, molecular, and physiological alterations. Cells and organisms can respond correctly to external signals and adapt to their environment thanks to these responses, which are essential for integrating and coordinating cellular activity.

4. Drought stress response genes

In general, functional genes and regulatory genes may be used to categorise genes involved in the drought stress response. Aquaporin genes, osmoregulatory factors (such as sucrose, proline, and betaine) synthase genes, and protective proteins (such as LEA protein, molecular chaperone, etc.) genes are examples of functional genes whose products directly resist environmental stress. In order to respond in an indirect way to stress, the products of regulatory genes such as protein kinase, protein phosphatase, phospholipid metabolism-related, and stress-related transcription factor genes are engaged in signal transduction and control of gene expression (Yang *et al.*, 2021). These proteins have an effect by taking part in pathways for the transmission of plant stress signals or by controlling the production and activity of other effector molecules.

A. Functional Genes

i. Osmotic Adjustment Related Genes

The associated enzymes may be categorised into three groups based on the various mechanisms of prolinebuildup. The first group includes the proline synthesis-related enzymes, such as ornithine-aminotransferase (-OAT), pyrroline-5-carboxylate reductase (P5CR), and -pyrroline-5-carboxylate synthetase (P5CS). Proline dehydrogenase (ProDH) and -pyrroline-5-carboxylate dehydrogenase (P5CDH) are the second category enzymes, related to degradation of proline enzymes. Proline transport-related enzyme (ProT) is the enzyme that belongs to third category. Cytoplasm and chloroplast are the sites, where proline is synthesised in plants, and glutamic acid (Glu) and ornithine (Orn) synthesis pathways are used in the process (Delauney & Verma, 1993). Ornithine synthesis pathway existed in nitrogen-abundant environments, but glutamic acid synthesis pathway mostly took place under osmotic stress and nitrogen scarcity (Hua *et al.*, 1997).

ii. Drought-Induced Protein Genes

LEA proteins are highly expressed during late embryonic development and play a crucial role in plant responses and resistance to drought. They function as molecular chaperones and hydrophilic solutes, capturing water and protecting the structure and function of proteins and membranes, thereby shielding cells from water stress (Hand *et al.*, 2011). For instance, Sivamani introduced the ABA-responsive gene HVA1, a member of the LEA protein group 3, into spring wheat and observed improved water use efficiency and growth characteristics in transgenic wheat under water deficit conditions compared to the control wheat (Sivamani *et al.*, 2000). In another study, transgenic plants expressing the CmLEA-S gene, a melon Y3SK2-type LEA gene, exhibited enhanced germination rates, increased seedling fresh weight, longer root length, reduced wilting and yellowing, elevated proline levels, decreased MDA content, and higher APX and CAT enzyme activities, demonstrating improved drought tolerance (Poku *et al.*, 2020).

Plant aquaporins (AQPs) are membrane channels found in the plasma membrane and intracellular compartments that facilitate the transport of water, small neutral molecules, and gases across cellular barriers (Kaldenhoff& Fischer, 2006). AQPs, belonging to the MIP protein family, regulate water movement and maintain water balance in plants, particularly under drought stress conditions. The major subclasses of AQPs are plasma membrane intrinsic proteins (PIPs) and tonoplast intrinsic proteins (TIPs), which play essential roles in intracellular water transport and the regulation of water relations during drought stress. For example, Zhang *et al.* (2019) discovered that the rose water channel protein RhPIP2;1 interacts with the membrane MYB protein RhPTM, influencing plant growth and stress responses. Over expression of CrPIP2;3, a PIP2 gene from rose, in Arabidopsis thaliana resulted in improved drought tolerance by regulating water homeostasis, leading to enhanced survival and recovery of transgenic plants under drought stress (Zheng *et al.*, 2021).

Here is a table summarizing some stress-responsive genes that are known to confer drought tolerance in plants, along with relevant references.

Table 2: Stress-Responsive Genes Conferred Drought Tolerance in Plants: A Summary and Relevant References

Stress-Responsive Gene	**Function and Contribution to Drought Tolerance**	**Reference**
DREB/CBF	Transcription factors that regulate the expression of stress-responsive genes	Lata *et al.*, 2011
LEA (Late Embryogenesis Abundant) Proteins	Protect cellular structures and macromolecules under stress conditions	Battaglia *et al.*, 2013
RD (Responsive to Desiccation) Proteins	Protect against dehydration and oxidative damage	Karim&Aronsson,2014
SOS (Salt Overly Sensitive) Pathway	Regulates ion homeostasis and maintains cellular osmotic balance	Fujita *et al.*, 2006
ABA (Abscisic Acid) Signaling Pathway	Controls stomatal closure, gene expression, and stress responses	Finkelstein *et al.*, 2002
SnRK (Sucrose Non-fermenting 1-Related Protein Kinase)	Regulates energy metabolism and stress responses	Halford *et al.*, 2003
AHK1/ histidine kinase 1	Positive regulator of osmo-sensing and drought tolerance	(Tran *et al.*, 2007)
NCED3/ 9-cis-epoxycarotenoid dioxygenase	key enzyme of ABA biosynthesis	(Takahashi *et al.*, 2018)
SNAC1, stress-responsive NAC transcription factor 1	drought avoidance and activation of transcriptional regulation of various other genes	(Saad *et al.*, 2013)
OSCA1/Hyperosmolality-gated calcium-permeable channel 1	membrane protein mediating osmotic stress responses	(Yuan *et al.*, 2014)
OsMYB2/ O. sativa MYB transcrption factor	drought avoidance and activation of transcriptional regulation of various other genes	(Yang *et al.*, 2012)

B. Regulatory Genes

The regulation of stress signal transmission and the expression of functional genes in response to drought are greatly influenced by regulatory genes. The following categories apply to these genes. First, transcription factors such bZIP, MYB, MYC, EREBP/AP2, CBFI (CRT/DRE binding factor), and DREB1A (DRE binding) are involved in controlling the expression of stress-responsive genes. Water stress has a powerful inducing effect on these transcription factors, which can further modify the expression of several functional genes. Second, protein kinases such receptor protein kinases, ribosomal protein kinases, and transcription regulatory protein kinases are involved in receiving and sending stress signals. In stress signal cascades, these kinases frequently function as amplifiers. The MAPK cascade is made up of three essential kinases that are important to the process: MAPK, MAPKK, and MAPKKK. The third group includes enzymes like phospholipase D and phospholipase C that produce and transfer second messengers. Phospholipase C catalyses the breakdown of PIP to create inositol triphosphate (IP3) and diacylglycerol (DG). Intracellular signal transduction activities start when IP3 causes the release of calcium ions (Ca^{2+}) from the endoplasmic reticulum into the cytoplasm (Yang *et al.*, 2021).

i. Signal Transduction Related Genes

Calmodulin, calmodulin-like proteins, calmodulin B-like proteins, and calcium-dependent protein kinases (CDPKs) are the four main families of calcium-binding proteins that are involved in signal transduction in plants. As Ca^{2+} signal sensors, CDPKs are essential for the continued transmission of cellular calcium signals. The EF-hand calcium-binding site is located in the carboxy-terminal calmodulin-like domain of CDPKs, which has an N-terminal serine/threonine protein kinase domain fused with it. This enables Ca^{2+} binding to directly activate CDPKs without the need for interactions with exogenous calmodulin (Cheng, 2002; Harmon *et al*., 2001). While the majority of CDPK genes are expressed in organisms by constitutive processes, others are expressed only in certain tissues or as a result of hormonal, biological, or abiotic stressors. The transcription of CDPK genes can be considerably increased by abiotic stressors as salt and dehydration (Botella *et al*., 1996; Patharkar & Cushman, 2000).

Moreover, drought, high salinity, and low temperature stress have all been observed to stimulate the MAP kinase genes identified from Arabidopsis thaliana, including AtMPK3, AtMPK4, AtMPK6, AtMEK1, and AtMEKK1. In addition to being controlled at the protein level by phosphorylation and dephosphorylation, the MAP kinase cascade system is also controlled at the transcriptional level in response to environmental stress signals. In response to mechanical stress, high salinity, low temperature, and drought, Mizoguchi *et al.* found that AtMEKK1 participates in the MAP kinase cascade signalling pathway in Arabidopsis. AtMEKK1, AtMEK1, and AtMPK4 are all MAPKK kinases that are involved in this cascade pathway (Mizoguchi *et al*., 1996).

ii. Transcription Factor Genes

Transcription factors (TF) play a critical role in the growth and development of plants under drought stress by regulating and reducing plant damage at numerous levels by activating different pathways throughout the signal transduction process (Shinozaki & Yamaguchi-Shinozaki, 2007). Among these, the HD-Zip/bZIP, AP2/ERF, NAC, MYB, and WRKY transcription factor gene families associated with drought stress are mostly to be found. However, depending on the plant species and strain, developmental stage, and intensity of the drought treatment, several transcriptional factors play various transcriptional regulatory functions in drought-stricken environments.

The HD-Zip transcription factors are a subset of the homeobox protein, which is made up of six families and encodes 60 conserved amino acid homeodomains (HD): HD-Zip, KNOX, PHD, BELL, WOX, and ZF-HD (Ariel *et al*., 2007). Among them, homeodomain-leucine zipper (HD-zip) is a DNA-homologous domain and extra Leu zipper (Zip) components that is a plant-specific transcription factor (Nakashima & Yamaguchi-Shinozaki, 2009). The former causes the production of protein dimer, a transcription factor important in controlling plant growth and development under normal growth circumstances and environmental stress, whereas the latter selectively binds to DNA (Harris *et al*., 2011).

Besides, the AP2/ERF transcription factors are crucial for plant stress resistance, and prior research has demonstrated that they may work in a variety of ways to help plants survive drought stress. By influencing plant hormone production, AP2/ERF can control the plant's response to drought stress. According to Cheng *et al.*'s hypothesis, ERF1 can integrate JA, ET, and abscisic acid signals through stress-specific gene regulation and contribute to drought tolerance since it is the upstream component of the jasmonic acid and ethylene signals (Cheng *et al*., 2013). AP2/ERF transcription factors play an important role in plant stress resistance and previous studies have shown that they can participate in the process of drought stress resistance in plants through different pathways. AP2/ERF can regulate drought stress response by affecting the synthesis of plant hormones. Cheng *et al*. (2013) proposed that as the upstream component of jasmonic acid and ethylene signals, ERF1 can integrate JA, ET, and abscisic acid signals through stress-specific gene regulation, and play a positive role in drought tolerance.

Additionally, the NAC family of transcription factors is a group of biologically diverse plant-specific transcription factors that is distinguished by highly conserved and distinctive NAC domains in the N-terminal of proteins. Through direct action or by controlling the expression of genes involved in drought response, NAC is crucial in enhancing plant resilience to drought stress. In plants under abiotic stress, Fujita *et al*. (2004) reported that RD26, a dehydration-induced NAC protein, has a transcriptional function in ABA-induced gene expression.

One of the biggest families of transcription factors in plants is MYB. It plays a significant part in the control of secondary metabolism, hormone and environmental responses, cell differentiation and morphogenesis guidance, and tolerance to drought and other abiotic stressors (Liu *et al*., 2015). It is also heavily engaged in the regulation of secondary metabolism. The 52 amino acids that make up the conserved helix-turn-helix (HTH) protein DNA binding domain at the N-terminus of the MYB transcription factor directly affect the precision with which it binds to target genes and can interact with cis elements including the GCC box, DRE, ABRE, and W box. The C-terminal is the transcriptional starting region and controls a transcription factor's ability to carry out transcriptional activity as well as how it interacts with other genes or components to affect the expression of genes downstream (Dubos *et al*., 2010).

Besides, the WRKY protein family is a zinc finger-type transcription regulator and a distinct transcription factor in plants. The WRKY domain particularly interacts with the (T) (T) TGAC (C/T) sequence (W box) of the target gene promoter in addition to at least one highly conserved WRKYGQK sequence and zinc finger structure (Eulgem *et al*., 2000). Many plant defence response-related genes have W-boxes in their promoters, and some WRKY transcription factor genes even have them in their self-promoters. In order to participate in the regulation of numerous physiological activities in plants, WRKY transcription factors may control the expression of downstream functional genes or other regulatory genes by interaction with W-box. By increasing proline and soluble sugar content, reducing ROS and MDA content, and boosting germination rate, root length, survival rate, and relative water content under stress conditions, TaWRKY10 over expression in tobacco improved drought resistance. This is due to TaWRKY10's beneficial effects on drought stress, which include controlling osmotic balance, scavenging ROS, and activating stress-related genes (Wang *et al*., 2013).

In summary, the mechanism of signal transduction in plants involves the reception of an external stimulus, transmission of the signal through signaling proteins, amplification of the signal through second messengers, protein phosphorylation, integration of multiple signals, regulation of gene expression, and subsequent cellular and physiological responses. This complex process allows plants to perceive and respond to environmental cues, including drought stress, in order to adapt and survive in changing conditions.

Conclusions

In conclusion, it is crucial to comprehend how plants tolerate drought in order to design ways to increase agricultural output and guarantee food security in the face of shifting climatic circumstances. The morphological, physiological, and biochemical pathways were the three main kinds of mechanisms that were the focus of this article.

By allowing plants to effectively use limited water resources, morphological processes play a critical role in drought resistance. These strategies, which prevent water loss through transpiration, include characteristics like deep root systems, smaller leaves, and thicker cuticles. Additionally, the growth of succulent tissues and the production of trichomes help drought-stressed plants retain and save water.

Complex physiological processes are part of the physiological systems that enable plants to adapt and endure in water-scarce environments. To stop water loss and preserve the water potential of the leaf, plants show stomatal closure. To sustain cell turgor and cellular processes, they also go through osmotic adjustments by collecting suitable solutes like glucose and amino acids. Additionally, plants activate signalling pathways that respond to stress, which control gene expression and increase drought resistance.

Biochemical pathways can improve a plant's resistance to drought stress by producing stress proteins like Drought-Induced Proteins (DIPs). These proteins help protect cellular structures and keep proteins stable. These proteins function as molecular chaperones and aid in preventing denaturation and aggregation of proteins in water-deprived environments. Oxidative damage can result from reactive oxygen species (ROS), which are byproducts of cellular metabolism created under drought stress. However, plants have antioxidant defence mechanisms that scavenge ROS, including peroxidases, catalases, and enzymes like superoxide dismutase.

Plants activate certain transcription factors and signalling molecules that control the expression of genes that respond to stress at the gene level. These genes are involved in a number of functions, such as osmotic control, ROS detoxification, and protein synthesis for defence. For the creation of genetically altered crops with increased drought tolerance, it is essential to comprehend the complex network of gene regulation during drought stress.

In general, a complex interaction of morphological, physiological, biochemical, and genetic elements is involved in the diverse processes of drought tolerance. Understanding these systems not only improves our comprehension of how plants adapt to water shortage, but it also provides important information for the creation of environmentally friendly agricultural methods and the breeding of drought-tolerant crop types. Future solutions to the problems of climate change and global food security depend on the continuation of this field of study.

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