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Adaptations and mechanisms underlying plant resilience to drought: Opportunities, challenges, and prospects for water-saving agriculture

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Abstract

One of the major obstacles to plant growth and productivity, outside of today's crop-growing zones, is drought. Due to acknowledged changes in the global climate, it will become more significant in areas of the world where the issue was previously insignificant. Considering the mechanisms underlying resistance to water deficit and the plants' effective water use is essential to addressing current concerns about enhancing plant genotypes and cultural practices for drought-affected locations. Main barriers to carbon uptake and the metabolic processes that influence how plants react to water scarcity, either alone or in combination with other stressors, are covered in this work. For crops that suffer from drought, oxidative stress is essential. Detoxifying mechanisms play a key role in preventing irreparable damage to redox molecules and photosynthetic machinery as a result of local or systemic signals. The ability of plants, particularly those that embed functional proteins, to prevent or fix membrane damage that occurs throughout the processes of dehydration and rehydration is essential to maintain the integrity of the membranes. These proteins include water transporters, whose function in controlling the water status of plants and moving other metabolites is being thoroughly studied. Over ten years ago, long-distance chemical signaling began to unravel as a primary response to water deficit. In light of new management strategies, the distribution and absorption of carbon and its assimilates among non-reproductive and reproductive parts are reviewed and examined. Enhancement of water-use efficiency in plants, consistent production, and better quality in products are all intended outcomes of these applications. It

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has already been feasible to discover important genes that can change metabolic processes, and boost the tolerance of plants to drying conditions by studying mechanisms underlying successful response to dehydration and rehydration. This study provides a summary of the most significant information on this subject, including water transporters and engineering for C_4 characteristics. Promising technologies, including the modification of crops by genetic engineering via the transfer of regulatory and functional genes, are highlighted.

Introduction

Water scarcity is one of the main obstacles for crop growth and productivity, outside of modern farming and agricultural lands, which drastically lowers crop yields (Batool et al., 2024). Irrigation and the utilization of suitable crops are major global issues since the forecasts for global environmental change indicate that drought, unpredictable weather, and extreme environments, and the frequency of extreme events will rise in different parts around the world in the future (Duan et al., 2024). Currently, about 40% food around the globe is grown on lands that have irrigation, while agriculture uses approximately 70% of the water that is available worldwide. About 10% of irrigation uses aquifer water, which results in the unsustainable exploitation of numerous subterranean water tables (Somerville and Briscoe, 2001; Abrar et al., 2024).

It is now known that increasing crop water-use efficiency through fine-tuning irrigation can result in more accurate water use while also improving product quality (Ullah et al., 2024). In a similar vein, contemporary biotechnology provides new instruments for sustainable and improved agriculture. While the primary agricultural innovations of the 1960s were created for favorable conditions, crop performance for less-than-ideal conditions and peripheral domains where the "onset of green revolution" was ignored has now become an important topic to be emphasized (Gui et al., 2024). Several studies have been done in the last several decades on the physiological and molecular underpinnings of how plants react in response to water deficit and other abiotic stress conditions such as extreme temperatures and radiation (Chaves and Oliveira, 2004; Batool et al., 2019).

Drying in plants can be caused by drought episodes or by a periodic drop in the accessibility of soil water that develops over time. Even irrigated crops' overall carbon gain is impacted by an enhancement in evaporation requirement by the environment, which primarily occurs daily. The impacts of drought are largely dependent on the occurrence, severity, and length of stress episodes. Plants regulate water levels and withstand drying conditions by different means (Ullah et al., 2024). According to Rehaman et al. (2025), genotypes that are indigenous to environmental conditions have a significant ability to respond to predictable climatic changes. These genotypes are generally capable of adapting to changing atmospheric situations, increasing the productivity of these genotypes, allied with the relevant surroundings. Plants may potentially shorten their life cycle to avoid dehydration in the event of slowly accumulating water deficiencies. Oxidative stress arising as a secondary result of rapid dehydration harms the photosynthetic apparatus (Ort, 2001; Liao et al., 2025).

Plant survival during drought is largely dependent on their ability to dissipate energy (Wang et al., 2023) and provide defense related to metabolism (either constitutive or induced) in response to harmful reactive oxygen species (ROS) effects (Batool et al., 2024). Although it is uncommon in many types of higher plants and other relevant crop species, tissue tolerance to extreme dehydration does develop in species that are indigenous to arid conditions (Li et al., 2014). Designing novel management techniques and genotypes for contemporary precision agriculture can be aided by an understanding of the mechanisms driving those disparate responses (**Figure 1**).

Reduced leaf carbon fixation (*A*) because of the closing of stomata is a well-known consequence of reduced water availability, and it can begin at moderate plant water shortages. The simultaneous or even earlier suppression of growth results in a further reduction of total carbon uptake at the plant level. Water stress has been demonstrated to directly impede cell expansion and division (Zhu, 2001). Because it enables plants to redirect energy and assimilation that would otherwise be utilized for growing the shoot, into defensive particles for combating stress conditions (Zhu et al., 2022), and to regulate the growth of root, and enhancement in the absorption of water, slower growth is proposed as an adaptive strategy for the survival by plants during water deficit (**Figure 1**). This characteristic could be irrelevant for areas where insignificant and irregular stress is expected to happen, but it might be important for reproductive plant species destined for less available water areas. However, in many crops, like pulses and some cereals, the capacity for storing (and then remobilizing) stem reserves is probably a crucial trait to sustain reproductive growth in the face of water shortages (Gui et al., 2020).

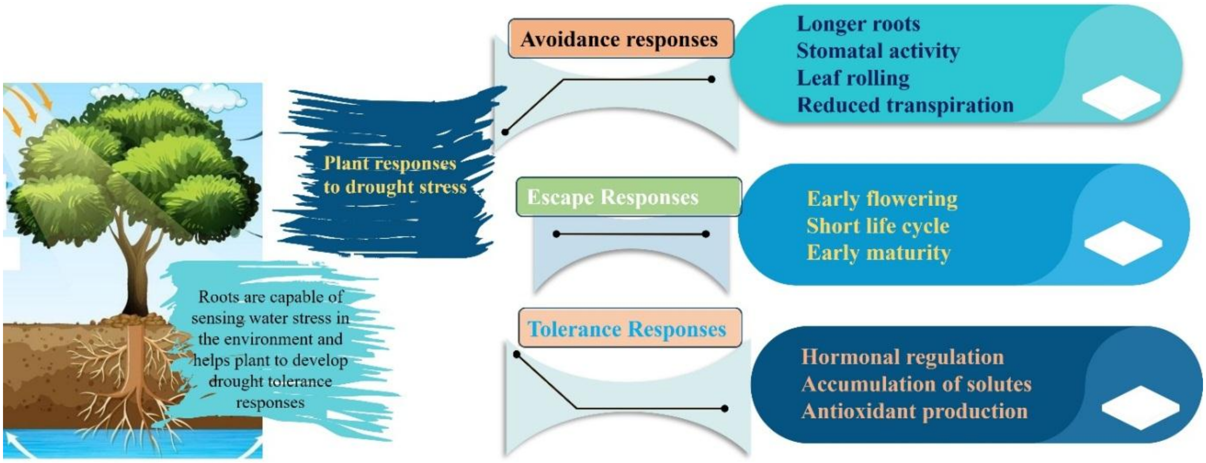

Figure 1: A schematic diagram showing the responses of a plant to drought stress, which can be categorized under Escape, Avoidance, and Tolerance

Revisions to limitations on regulatory and photosynthesis mechanisms that function under water deficit

Diffusive and metabolic constraints: intercellular CO_2 functions as a modulator of metabolic changes

Even though there has been ongoing discussion over the type and timing of the restrictions that drought place on the uptake of carbon by leaves (Nasir et al., 2019), specifically about non-stomatal versus stomatal limitations, it is widely acknowledged that stomatal closure is the primary cause of the decline in photosynthesis that occurs in response to mild soil and/or atmospheric water shortages in field settings (Luo et al., 2020). Nevertheless, primary biochemical consequences of water shortages include changes in photophosphorylation (Tezara et al. 1999; Liao et al., 2025), but it is not often acknowledged, as it is the main delicate constituent of photosynthesis in response to drought. Studies have demonstrated that it takes extremely severe dryness before photosynthesis is restricted by a decline in the activity of Rubisco and levels of RuBP (Khan et al., 2025).

The capacity to transport electrons, one of the primary processes of photosynthesis (Opoku et al., 2024), and changes in substrate availability can account for fluctuations in PSII photochemistry. Indeed, during water stress, φPSII frequently decreases in tandem with photosynthetic efficiency (A), indicating that the electron chain's activity in photosynthesis is associated with the uptake of CO_2. It has already been discovered that a quick switch to an environment rich in CO_2 could nearly overcome the decline in the effectiveness of photochemistry seen in leaves either treated with ABA or desiccated (Burkart et al., 2011). This suggests that the capacity of photosynthesis endured greater during drought, where the primary cause of the decline in net uptake rate of carbon during the photosynthesis process has been CO_2 constraint. The metabolic aspect of photosynthesis decline that persisted after the rapid shift to an increase in atmospheric CO_2 may be explained by the inactivation of Rubisco, the carboxylating enzyme, caused by lower Ci (intercellular CO_2) (Cao et al., 2022). Reduced intercellular CO_2 may be a key mediator of biochemical changes in photosynthesis (Ort et al., 1994). Vassey and Sharkey (1989) claimed that the biochemical consequences of water stress appear to primarily target SPS (sucrose-phosphate synthase), an extremely controlled enzyme which is essential to plant source-sink connections. The SPS activity was found to diminish after closure of stomata, and a decline in leaf CO_2 content in intercellular airspaces. According to Maroco et al. (2002), who used the A/C_i analysis to estimate the limitation of A under the effect of triose phosphate studied in grapevines, this outcome might result in constraints in assimilation of carbon by Pi during drought. Nevertheless, this effect can be undone by raising the amount of CO_2 in the surrounding environment (Wang et al., 2018). An earlier study has discovered that nitrate reduction in spinach leaves was repressed during stomatal closure when there was a mild stress (Han et al., 2023). The present constraint was inverted, and the decline in nitrate proceeded normally when those leaves were exposed to an environment containing 15% CO_2.

According to another study conducted on many species experiencing drought, metabolic degradation of photosynthesis does not happen until the maximal light-saturated response of stomatal conductance is extremely small (Medrano et al., 2002). This supports the idea that drought-induced metabolism is impacted by CO_2 scarcity. However, the mesophyll's enhanced resistance to diffusion of CO_2 during water deficit showed limited photosynthesis and does not earn adequate consideration (Bellasio, 2025). Actually, according to various scientists, CO_2 encounters other diffusive limitations on its journey from the environment to the cell chloroplasts, rather than only the resistance in stomatal conductance. According to other studies, the resistance of the mesophyll to transferring CO_2 could be significant enough to reduce the concentration of CO_2 from C_i (intercellular spaces) to C_c (site of carboxylation). If this resistance is ignored, it can also result in an overestimation of the metabolic constraints on carbon assimilation (Busch, 2020).

Along with water deficit, plants are frequently exposed to many challenges in the field, such as intense heat and light (Gui et al., 2024). Plants are at risk of photoinhibition or a down-regulation of photosynthesis when increased irradiance is combined with CO_2 deficiency in the cell chloroplast, and this CO_2 deficiency occurs due to stomatal closure. In fact, at a rate where power production decreases can outpace the rate at which the Calvin cycle uses it when CO_2 fixation is restricted. Under water stress, protection processes that stop the generation of surplus power are therefore a crucial tactic. The controlled thermal dissipation that takes place in the complexes of light-harvesting, which involves the xanthophyll cycle (Bellasio, 2025) and most likely the lutein cycle (Busch, 2020), may provide this kind of protection. The reduction in PSII quantum yield indicates a down-regulation of photosynthesis as a result of these photoprotective systems competing with the mechanism of photosynthesis and light reactions and the energy that is already absorbed (Genty et al., 1989). If an additional sink for the absorbed energy becomes more active in tandem with the rate of CO_2 assimilation being limited, such as photorespiration (Zhou et al., 2004) or the Mehler-peroxidase reaction (Yi et al., 2016), compared to the reduction in the rate of assimilation of CO_2, the reduction in non-cyclic process of transport of electron would be relatively smaller. This kind of reaction has mostly been observed in plants that are indigenous to semi-arid areas. The way that agricultural plants respond to extreme light, which can occur even in summertime in plants that are grown in irrigated fields, is far less understood.

Does drought cause oxidative stress or redox signaling?

Crop survival during a stressful event, like drought and high temperatures, is crucial in agriculture. Rapid activation of protective mechanisms at the leaf level is necessary to avoid irreversible damage to the photosynthetic machinery. Signals are therefore important for plants' ability to withstand stress (**Figure 2**).

As previously stated, after a sharp drop in intercellular CO_2 during drought, the electron transport chain's components over-reduce, causing electrons to be converted to oxygen (O_2) at photosystem I (PSI) or by Mehler process. Photo-oxidation may result from the reactive oxygen species (ROS) produced due to this mechanism, including hydrogen peroxide (H_2O_2), hydroxyl radical ($OH^{\cdot}$), and superoxide ($O_2^{\cdot}-$), if these chemicals are not effectively scavenged by the plant. We now know that the redox status of the electrons involved in photosynthesis reactions and the redox-active compounds that are produced also function as metabolic regulators (Batool et al., 2024).

Signaling by redox affects a leaf's energy balance and serves as an early warning. Several genes related to photosynthesis (in the nucleus and the chloroplast) are expressed differently depending on the redox state of redox-active substances. Hence, serving as the foundation for photosynthesis's feedback response to the surroundings, or, to put it another way, the balancing of energy consumption and production, it should be noted that there is still conflicting evidence about the redox control of genes involved in photosynthesis, pointing to a very intricate signaling network (Pfannschmidt, 2003). Some important electron carriers, such as the PQ (plastoquinone pool), thioredoxin, and ferredoxin system, are counted as electron acceptors, and reactive oxygen species, such as hydrogen peroxide, are examples of redox signaling molecules. It has been demonstrated that the redox state of plastoquinone regulates transcription of genes that are involved in photosystem response centers of chloroplasts and cyanobacteria (Midorikawa et al., 2009). Specifically, photosystem I reaction center's transcription is activated by a decline in plastoquinone, while the photosystem II reaction center's transcription is activated by an oxidized pool, respectively (Yi et al., 2016).

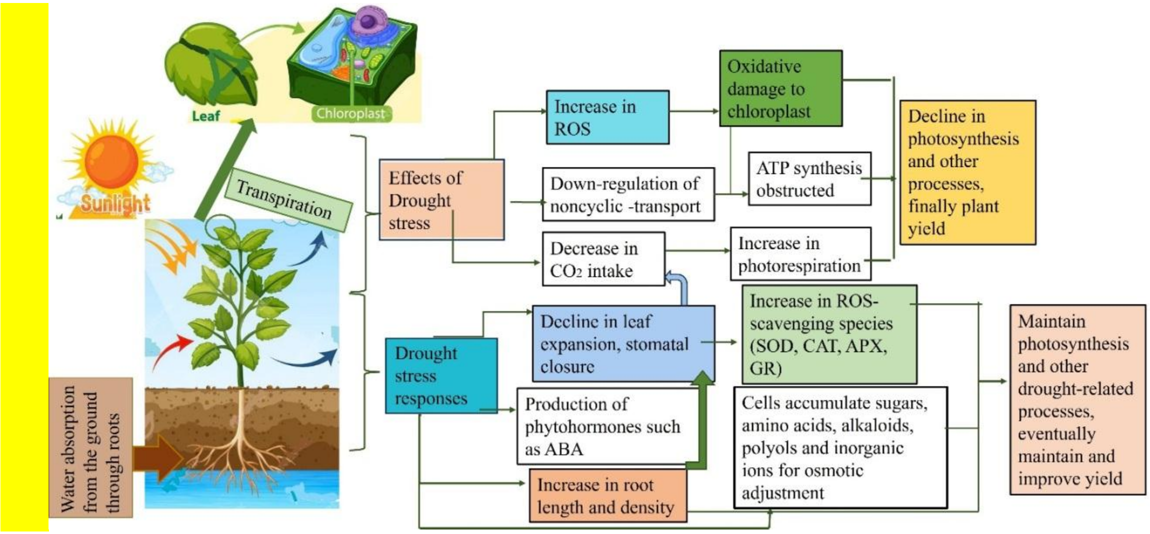

Figure 2. A schematic diagram showing the various effects of drought stress on plants and their adaptive responses. ABA, Abscisic acid; ROS, Reactive oxygen species; SOD, Superoxide dismutase; CAT, Catalase; APX, Ascorbate peroxidase; GR, Glutathione reductase; ATP, Adenosine triphosphate.

Glutathione and ascorbate pools are part of the plant purifying mechanism that regulates intracellular reactive oxygen species concentrations. According to mounting data, these substances are involved in the transduction of redox signals and function as secondary messengers in hormonally mediated processes, specifically stomatal movements (Nasir et al., 2020).

Heat shock proteins are induced, leaf stomata close, and leaves acclimate to higher irradiance when H_2O_2 is present as a systemic or local signal (Rogers and Munné-Bosch, 2016). In *Vicia faba*, it was initially documented that H_2O_2 can affect the guard cells (McAinsh et al., 1996). They discovered that exogenous H_2O_2 applications caused stomatal closure and an increase in cytosolic calcium. However, it has been demonstrated that applying ABA to *Arabidopsis,* the guard cells cause an H_2O_2 burst, which in turn causes closure of stomata (Wang and Song, 2008). Nevertheless, programmed cell death may occur if H_2O_2 production surpasses a threshold.

As a link between symplast and atmosphere, the apoplast's perception of stress is significantly influenced by H_2O_2 and other redox substances. Aquaporins have recently been found to carry H_2O_2 from apoplast to cytosol, indicating that transduction of signals could likewise be regulated by altering transport networks (Pastori and Foyer, 2002; Wang and Song, 2008). The interaction between the antioxidants, especially AA (ascorbic acid), and the signaling oxidants, the apoplast's primary buffer for the redox status, is essential for controlling how plants grow and respond to abiotic and biotic stressors (Pignocchi and Foyer, 2003). According to these scientists, the stress response results from changes in receptor function and signal transduction caused by alteration of the apoplast redox state. Additionally, it was recently proposed that the apoplast's AA and the enzyme that controls its redox status, AO (ascorbate oxidase), have a role in expansion and division of the cell, two mechanisms which typically impacted due to a variety of stressors, including drought. For instance, when an oxidized form of AA (DHA), builds up in the cell apoplast, cell division is inhibited (Dietz et al., 2016).

By modulating hormone effects and further key molecules that are involved in signaling in response to ecological stimuli, NO (nitric oxide), one of the components of ROS, functions like a signaling molecule. It might work by making cells more sensitive in response to substances (Ullah et al., 2024). It has been demonstrated that nitric oxide functions as a mediator of the effects of abscisic acid on leaf guard cells (Dietz et al., 2016). Similar to H_2O_2, nitric oxide plays a role that how the apoplast perceives stress because this section may perform as a key location for the production. Hydrogen peroxide (H_2O_2) and NO might be produced simultaneously, then work together to produce a variety of physiological reactions, such as stomatal reactions to environmental stressors (Rogers and Munné-Bosch, 2016). While the exact relationship between dehydration and NO is still unclear, it appears that protein kinases, calcium, and cyclic GMP are some of the signaling elements downstream for H_2O_2 and NO for closing of stomata that is induced by ABA (Desikan et al., 2004). After networking with reactive oxygen species, generated due to various stressors, including superoxide, which prevents peroxidation of lipids, nitric oxide also acts as an antioxidant. However, excessive NO production can lead to nitrosative stress (Ullah et al., 2024). Additionally, several important physiological responses, such as programmed cell death, appear to be influenced by the equilibrium between NO and H_2O_2.

Nitric oxide generation, depending on the NR (Nitrate reductase), is currently gaining a lot of attention since nitrite can function as a precursor of NO. The atmosphere, including light, nitrate supply, cytosolic pH, CO_2, and temperature, greatly influences NR activity, which can be seen in nitric oxide generation and directing actions, like those applied to the opening of stomata (Sun et al., 2019). Additionally, a proposal was forwarded that nitric oxide may function in extended places, such as by sending nitrite to shoot, from roots through the stream of xylem. In the guard cells, it would subsequently generate NO. According to this data, NR may also be involved in controlling the response of stomata to ABA production, along with other stressors in addition to its function in coordinating the conversion of C to N.

Lastly, NO appears to contribute to the way roots react in response to an eater deficit and further abiotic stress factors via promoting the formation of adventitious roots (Ma et al., 2020).

Signaling by sugar molecules

Water deficiencies change the amount and quality of the leaf's carbohydrates, which could serve as a metabolic indicator under drought stress (Batool et al., 2018). In this aspect, sugar’s function as a signaling molecule is not entirely evident. Overall, water deficit could result in a higher amount of leaf soluble sugars (under moderate stress) and/or a stable concentration (in response to acute drought), despite decreased carbon absorption, because it also inhibits growth and export. Soluble sugars may decrease in extremely severe dehydration (Pinheiro et al., 2001). Even with mild water deficiencies, starch production is generally severely reduced (Chaves, 1991).

Rapid glucose and fructose buildup in maize leaves was accompanied by an increase in acid invertase activity in the leaves of drought-stricken plants (Cardoso et al., 2020), coupled with the buildup of sucrose, fructose, and glucose in *Citrus sinensis* leaves, roots, and stem (Huang et al., 2022). In contrast to the fluctuations in leaf blades, there is a tendency for variations in the sucrose of the leaf petioles, indicating that under extreme stress, leaves export more in wheat plants (Kang et al., 2023). Remarkably, there was a strong correlation between the ABA content in xylem sap and the action of acid vacuolar invertase. According to another study, ABA significantly increases the expression and activity of IVR2 vacuolar invertase (Chaves and Oliveira, 2004). Additionally, evidence showed that ABA production is directly controlled by glucose. In *Arabidopsis* seedlings, it was found that glucose increased transcription for many genes that are associated with ABA production (Cheng et al., 2002). There have also been reports of ABA and glucose altering the expression of ABA signaling genes. According to additional data, environmental cues, including water, light, and CO_2, can be combined and interpreted as sugar signals (Liao et al., 2025), indicating that the signal pathways unite downstream or that the same receptor may perceive diverse signal forms (Rehaman et al., 2025). Conversely, sugars that move through the xylem of plants that are experiencing drought or that may significantly rise in guard cells’ apoplast when exposed to intense light are expected to have a significant impact on the sensitivity of stomata in response to ABA synthesis (Chaves and Oliveira, 2004; Khan et al., 2025).

It was also discovered that there was crosstalk between the sugars and other hormones of plants, such as ethylene and ABA (Liao et al., 2025). For instance, it is demonstrated that whereas ABA and glucose can stimulate growth at low doses, they work in concert to suppress development at high quantities. However, it was shown that ethylene might counteract the growth inhibition caused by glucose, even though this hormone generally inhibits growth (Leon and Sheen, 2003). Antagonistic ABA’s effects on root and shoot growth are an example of how responses and interactions seem to depend on specific tissues as well as concentrations (Sharp, 2002).

Additionally, sugars interplay signaling crosstalk and control the numerous genes which are associated with the metabolism of nitrogen and lipid, along with biotic stress (Smeekens and Hellmann, 2014). Through a branched and complex process, sugars influence gene expression that codes for the pathway of photosynthesis. Sugar accumulation results from a decrease in the consumption of photoassimilates, while sugar depletion causes an increase in photosynthetic activity, most likely because sugar controls on transcription are derepressed (Pego et al., 2000).

The significance of membrane stability in chloroplasts confrontation to rehydration and dehydration

Higher plants can somewhat cushion the changes in plant water status, in contrast to poikilohydric plants, which alter water potential of their tissue in tandem with air and soil relative humidity with that of the soil and/or air and recover rapidly upon rehydration. This could be accomplished, as was previously said, by either enhancing the acquisition of water during drought through the mechanism of osmotic adjustment in the root or by making an extra deposition in the system of roots, or by avoiding loss of water through stomatal closure.

Sufficiently severe water deficits (usually defined as having a leaf *RWC* below 70%) (Batool et al., 2023) or too protracted can cause wilting of leaves, shrinking of cells, and membranes to experience power-driven pressure. One of the most significant consequences of extreme water deficit and existence is the stress on membranes since membranes are essential for many biological processes, especially those that include ion transporters, water, and enzymes embedded in them. The ability of plants to prevent or amend membrane injury and preserve the solidity of the membrane at the time of rehydration and dryness processes is directly related to recovery under these circumstances. It is discovered in wheat leaves that photosynthetic sheaths deteriorated formerly (became temporarily penetrable) from the plasma membrane, then wilted more slowly in the natural environment (Zhao et al., 2020). Since chloroplastic membranes can generate significant amounts of reactive oxygen species (ROS), in addition, membrane-bound components of chloroplasts remain particularly vulnerable to oxidative stress. Protein denaturation, DNA mutation, and widespread membrane lipid peroxidation and de-esterification can all be brought on by ROS (Bowler et al., 1992). However, severe shrinkage increases the internal solute concentration, which can approach poisonous levels for some enzymes and proteins (Wang et al., 2018). This exacerbates the negative effects on the cytosol, other organelles, and photosynthetic apparatus. Cell contents become viscous as cellular volume decreases, which raises the likelihood of molecular interactions that might result in membrane fusion and protein denaturation (Oliver et al., 2020).

Remarkably, research on oxidative stress has revealed certain antioxidants and/or their transcripts (such as ascorbate peroxidase, or APX, or glutathione reductase, or GR), which might be greater during retrieval time as compared to the water deficit time (Wang and Song, 2008). This could indicate that protection by antioxidants is essential throughout the phase of recovery, or that strain might have triggered a response to antioxidants that "stabilizes" the adaptive mechanisms of plants to upcoming stress situations (**Figure 2**). Numerous substances have been found to have protective effects on macromolecules and membranes. They include fructans, polyols, trehalose, sucrose, oligosaccharides, glutamate, mannitol, proline, carnitine, sorbitol, and glycine-betaine etc. Each of these substances helps the proteins stay hydrated (Hoekstra et al., 2001). The water linked to the membrane macromolecules may be replaced by sugars after additional drying, preserving the structural integrity of the molecules. Specifically, the hydroxyl groups maintain hydrophilic connections with membrane lipids and proteins by substituting water. By replacing hydrogen bonds and sequestering ions, dehydrins are thought to stabilize membranes and shield proteins from denaturing agents (Close, 1996). During the dehydration and rehydration processes, small heat shock proteins (HSPs) may function as molecular chaperones. In general, HSPs can keep partner proteins folded-competent, which reduces the number of non-native proteins that aggregate and breaks them down, and eliminates these proteins from the cell (Wang et al., 2004). The best solutes for maintaining membranes and proteins at small water contents are sugars, particularly non-reducing disaccharides, as likewise fructans, tetrasaccharides, and trisaccharides. The hydrophobic effect that gives macromolecules their form and function is lost at this H_2O concentration, because H_2O disappears from their H_2O shell (Hoekstra et al., 2001).

According to Zhao et al. (2020), rapid rehydration caused more damage to the membrane (specifically, the chloroplast envelope) than the previous dehydration practice. A temporary membrane leak occurs when water replaces sugar (or another suitable substance) at the membrane surface during rehydration (Hoekstra et al., 2001). When dehydration is severe enough to cause some membrane rigidity, an irreversible leak occurs, which is followed by fatal damage. Membrane fluidity appears to have a significant role in the confrontation to damage. The delayed recovery following rewatering, which is frequently seen during extended and/or severe drought, may be explained by rehydration effects on membranes. Additionally, it was proposed that species-specific differences exist in the level of reversibility of dehydration's effects. This may be more indicative of variations in leaf structure than species-specific metabolic variations (Du et al., 2025).

Signaling at long distances: the fundamental/root chemical signals

There has long been discussion about the significance of biochemical/chemical cues produced in plants' roots for anticipated reaction under drought (Wilkinson and Davies, 2002). Chemical substances must move throughout the plant as a reaction to soil drying detected by roots, in response to root-to-shoot signaling, to happen. These signals could be adverse/negative, if anything is removed from the flow of xylem, or positive if something is introduced to the xylem stream.

Under unfavorable development circumstances, for example, differences in nutrients, water, and light, accessibility, hormones might play a substantial role in controlling the metabolism of the plant. In these situations, developmental plasticity may be advantageous because it may result in altered growth that maximizes the plant's response to its surroundings (Trewavas, 1986; Lv et al., 2019). The root-shoot signaling process has been linked to hormones, specifically ABA, but also cytokinins and ethylene, which can work alone or in tandem. ROS might have an important function in this hormone's long-distance signaling, like as a mediator (Lake et al., 2002; Batool et al., 2024). In xylem sap, enhanced concentration of cytokinin has been demonstrated to directly endorse the opening of stomata and reduce stomatal sensitivity to ABA, which is an illustration of signaling cross-talk of hormonal responses, in root-to-shoot signaling (Liu et al., 2014). Recent reviews on the fundamental role of ABA in these combined mechanisms have covered a wide range of topics, including biosynthesis, cell/tissue compartmentation, factors-based modulation, and response coordination at the whole plant level (Liao et al., 2025). It has been demonstrated that chemical substances produced in drying roots, specifically ABA and/or its conjugates (glucose esters), function as long-distance signals that cause closure of leaf stomata, or limiting the growth of leaves by discontinuing the meristematic process, since the middle of the 1980s (Blackman and Davies, 1985; Batool et al., 2024; Rehaman et al., 2025). This understanding has made it possible to comprehend how certain plant reactions to soil drying can take place without causing appreciable alterations in the water status of the shoots. In this instance, "isohydric" plants can regulate stomatal aperture through feed-forward mechanisms, buffering their leaf water potential.

Additional research has demonstrated that the environment can affect transport of ABA into xylem of roots, specifically via xylem pH, where guard cell responses to ABA and pH variations appear to be time-dependent (Chaves and Oliveira, 2004; Rai et al., 2024). Loading of ABA to root xylem can be improved with an incline in xylem pH that could happen under soil drying (Batool et al., 2018). Water stress may also increase the ABA root signal by decreasing catabolism of ABA and preventing phloem and rhizosphere-ABA from inflowing to symplast (Li et al., 2022). Environmental factors that promote transpiration, like VPD, also raise the pH of leaf sap; these increases in leaf sap pH are linked to decreases in stomatal conductance. Species differences in ABA sensitivity for the stomata may be linked to varying levels of alkalinization under drought conditions (Chaves and Oliveira, 2004). However, as observed in tomato and barley ABA-deficient mutants, an increase in the pH of xylem sap might function alone as a water deficit signal to decrease leaf growth through an ABA-dependent process (Karuppanapandian et al., 2017).

Sharp (2002) suggested, ABA plays an indirect function in regulating the growth of root and shoot by reducing the synthesis of ethylene. Since ethylene limits growth, a lack of accumulation in ABA might allow shoot growth to be inhibited by ethylene, while a higher ABA accumulation in roots would stop the ethylene-mediated growth inhibition. ABA translocation from roots to shoots, along with causing closure of stomata and, thus, turgor maintenance, would partially offset the suppression of shoot growth by ethylene (Sharp, 2002). Taking into account that ABA eventually coordinates the performance of the entire plant by controlling the assimilation distribution between root and shoot, whereas a common hormonal function known as "resource allocation" could be used to characterize this long-distance signaling of ABA (Batool et al., 2024; Liao et al., 2025).

Water-saving agricultural applications

Enhancing the trade-off between water and absorbed carbon in plants through the use of regulated irrigation

Knowing the variables that control the trade-off between water loss and carbon absorption, and the mechanisms that influence the division of assimilation between non-reproductive and reproductive structures in response to the availability of water, are crucial for determining the technology that will balance plant needs with water input (Duan et al., 2024). A growing number of irrigation techniques are being employed to increase agricultural water use efficiency (Zhang et al., 2020) while maintaining or improving the quality of the product by taking advantage of a long-distance signaling system in plants (Batool et al., 2019). It was shown that controlling stomatal functioning can conserve water and that high, uncontrolled water fluxes are not necessary for the functioning of the plant (Xiong et al., 2006a). Plants' capacity to sustain symmetry amongst the prevailing procedures, specifically light harvesting, CO_2 diffusion, biochemistry and photochemistry, is a sign of effective control of carbon acclimatization under fluctuating water supply, so that, aside from brief transitional times, the flow through each process component is balanced through others (Xiong et al., 2006b).

Stomatal conductance in leaves often drops more quickly than carbon absorption when water deficits begin to accumulate, and ultimately leads to enhanced WUE (water use efficiency) (Lv et al., 2019). Additionally, it is well recognized that unnecessary growth of the shoot may happen at the expense of fruits and roots when irrigation is above optimal (Zhang, 2004). Crop water use before and after flowering can be manipulated to raise the harvest index (HI), and stomata's optimal water use through controlled irrigation techniques can raise WUE without significantly lowering production and eventually improving quality.

When the leaf itself experiences water deficiencies, the stomata close. This can happen as a feedback reaction that is communicated to the guard cells, or from a feed-forward regulation before the water state of the leaf tissue changes (Batool et al., 2018). There is an ongoing discussion over the processes underlying these guard cell feed-forward processes to high vapour pressure deficit, while in the meantime, other parts of the plant, specifically the roots, are experiencing dehydration (Franks and Farquhar, 1999). At the very beginning of drought, shoot growth is slowed down in conjunction with stomatal closure (Lv et al., 2019). There is substantial evidence, as was covered in the preceding section, that long-distance signals generated in drying roots may facilitate this type of reaction to declining soil water, specifically chemically derived (like cytokinins or ABA) and carried to the shoot through the transpiration stream (Batool et al., 2019). A portion of the water present in the soil will be supplied to the shoot by them. Nevertheless, ABA signaling is a multifaceted process that includes not just the up-regulation of production of ABA and its movement to the leaf through the xylem, then eventually depends on the changeable function of trapping of anion and the xylem sap homeostasis across the way of transport system (Karuppanapandian et al., 2017). In actuality, ABA filtering occurs in the leaf cells, where a significant amount of the ABA carried from the roots is broken down (Wilkinson, 2004). It has been demonstrated that ABA cannot enter the apoplast through the xylem due to the leaf apoplast and xylem sap pH. The "anion trap" theory is the foundation for this, proving that ABA builds up in the cells' utmost alkaline sections. Therefore, the apoplastic pH ultimately controls the onset of these signals at the developing tissues or at guard cells (Chaves and Oliveira, 2004). The final apoplastic pH is determined by the interaction of environmental elements (e.g., temperature, VPD, or PPFD) that affect shoot physiological processes with rhizosphere-affecting factors. Plant WUE will therefore be a reflection of the various environmental cues that are sensed as well as the genotype's capacity to detect variations in the availability of moisture and adjust its status of water status accordingly (Wilkinson, 2004).

This information has led to the development of a unique system of insufficient irrigation recognized as PRD (partial root-zone drying), in which the root system's two sides receive alternating irrigation durations. In PRD, the wet portion of the system of root ensures that the plant's water status is maintained, while the drying roots encourage stomata to close, which reduces water consumption (Davies et al., 2000). Australia has already implemented the PRD irrigation system in yards of vine on a large scale (Romero et al., 2022). Grapevines and more crops like raspberries, tomatoes, olive trees, or orange trees have all been the subject of additional research on this type of irrigation (Bellvert et al., 2020). It is acknowledged that closure of stomata and inhibition of growth are probably reacting to various stimuli at the same time, even though the exact nature of the signals is unclear. Some of these stimuli may function through similar signaling transduction pathways (Huang et al., 2019). There are minor distinctions between PRD and deficit irrigation (DI), in which the two sections of the root structure distribute the same quantity of water, according to physiological data that is being gathered (for example, in grapevines under PRD) (Romero et al., 2022). These variations comprise a decrease in vegetative growth, an increase in bunch exposure to radiation of sunlight, and a slight decrease in stomatal aperture in PRD (which is more noticeable when stomatal conductance measurements are made in a setting with consistent temperature and light as opposed to one with changing conditions in the field). These changes may also improve the quality of the fruit. The relationship between VPD and the strength of the PRD stomatal response is an intriguing discovery; a greater *VPD* intensifies closure of stomata with PRD in comparison to control treatments (Fereres and Soriano et al., 2007). According to various findings, it is suggested that a greater capacity of the xylem to provide ABA may be connected to the improved stomatal response to VPD in PRD irrigation.

Additionally, PRD has been shown to improve tomato fruit quality, most likely due to its distinct impacts on reproductive and vegetative output (Alemu, 2020). Partial dehydration also appears to cause a considerable change in the architecture of the root system, in addition to changes in its biomass and total extension (Batool et al., 2018). Plant performance under PRD is probably significantly impacted by this change in the root properties and the balance between the source and sink.

Reserves built up in the stem before anthesis in certain crops, like legumes and some cereals, could be used for the grain filling process, together with the assimilates present, leading to significant increases in HI (Kang et al., 2021). Stem deposits are necessary to finish filling of grains in stressful situations or at greater respiration rates (such as higher temperatures) (Gent, 1994). Although stem length and weight density are important factors in determining the possibility of retaining reserves in the stem, they are insufficient to guarantee that those reserves will be transferred to the fruit. Reserve mobilization is reliant on sink strength, which is genotype-specific and is influenced by environmental factors (such as water availability). However, the stem is particularly well-protected from environmental stress, especially the stele part of the stem, which is connected to vascular tissues (Wang et al., 2020). Indeed, research on drought-imposed lupins showed that the stele of the stem did not once decrease its RWC (relative water content) lower than 83%; in contrast, the other organs of the plant stem cortex 58%, the roots 58%, and leaves 57%, showed values below 60% (Pinheiro et al., 2004). It is hypothesized that this reaction is linked to the defense provided by the buildup of assimilates, primarily sucrose, glucose, and fructose, whose content in the stem stele doubles during drying conditions (Pinheiro et al., 2001). Additionally, these sugars may serve as cues for the protective proteins, like as LEA (late embryogenesis abundant) proteins, which are seen to be induced more strongly in the stele as compared to the cortex.

It has been demonstrated that controlled water deficit improves HI and encourages the carbon stocks remobilization all through late grain filling in wheat, particularly as plants are grown at higher nitrogen conditions (Yang and Zhang, 2006). Actually, in these circumstances, a slight drying of the soil enhances the stem deposits to grains and counters the interruption in vegetative tissue senescence, which often follows extensive N usage. A prolonged period of stay-green causes the pre-anthesis stores in stems, leaves, and glumes not to be remobilized. These reserves may be responsible for 8–27% of carbon deposited in grain in the form of carbohydrates and 30–47% of the carbon into protein (Fang et al., 2024). Delays in crop maturation can cause dry winds at the end of the growing season to quickly dehydrate the wheat in China, lowering grain production. Yang et al. (2001) demonstrated that they could speed grain filling and increase production by imposing a medium water deficit, which thereby caused an early aging.

However, in areas free of the aforementioned restrictions, the prolonged phase of grain filling and so postponing senescence in the leaf may increase productivity by giving assimilates more time to translocate towards the grain (Sadras and Richards, 2014). Either managing irrigation or choosing genotypes with stay-green potential can accomplish this.

Recent developments in genetic engineering for enhanced plant response to water deficiency

The majority of effective genetic engineering projects in agriculture over the last ten years have focused on improving technological qualities or crop resilience to biotic stresses (Sonnewald's 2003). To date, research on plant resistance to abiotic stress, specifically drought, has been limited to single gene methods and experimental laboratory work, which has resulted in very modest improvement against stress (Ost et al., 2023). Current developments, nonetheless, indicate that quick advancements would be feasible soon, with significant economic effects in numerous parts of the world. Even small gains in WUE (water-use efficiency) and crop adaptation to drying conditions will boost production and conserve water (Gui et al., 2020). Developing plants that can grow in challenging environments and produce a respectable amount of biomass while also surviving stress is one of the main encounters, and is being faced by this technology, resolving the negative relationship that previously existed in earlier breeding programs between drought-resistance characteristics and efficiency (Mitra, 2001). Improved effectiveness in preserving homeostasis, purging cells of toxic substances (such as ROS), and resuming growth that has been halted due to acute osmotic stress are all necessary for such a compromise (Xiong and Zhu, 2002). This implies that sets of genes that control quantitative features must be introduced. This is a technical approach that has already shown effectiveness, as seen in the illustration of transgenic rice that has been supplemented with A provitamin (Beyer et al., 2002). The genetic basis of stress tolerance may be represented by these genes, as evidenced by the progressive cloning of several stress-related genes and response molecules, and the evidence linking them to stress-tolerant quantitative trait loci (QTLs). However, a key technique for MAS (marker-assisted selection) of tolerant plants is the discovery of QTLs linked to water deficit tolerance. A wide range of species have been the subject of these investigations (Poretti et al., 2023; Sarkar et al., 2023). There has been a lot of research performed on this subject, which would not be entirely discussed here, but it is obvious, combining molecular and old-style breeding, for example, genetic engineering and MAS, would enable a quicker method of enhancing crops' resistance to abiotic stress; it is being used to create plants with greater tissue tolerance to desiccation or drought avoidance traits by utilizing our growing understanding of stress adaptation mechanisms and the discovery of important pathways and connections included in the response of plants to water deficit (Laporte et al., 2002). Since the earlier is tied to the morphological and physiological traits of the entire plant, it is more challenging to accomplish (Altman, 2003).

The potential in engineering for designing significant features, through the alteration of downstream signaling processes, and the usage of a single gene that may affect several stress types, is increasing due to recent advancements in the discovery of genes and understanding of signal crosstalks and their interplay. Furthermore, in genetic engineering, it's critical to emulate nature and only trigger the genes required to shield plants from the negative impacts of stress at the appropriate time. This will reduce effects on development in situations without stress, which is crucial for agronomic plant species, and can be accomplished by employing suitable stress-inducible promoters. To prevent adverse consequences, it is also preferable to mark the specific tissue or cell site, regulate expression's strength and timing, and make sure that all metabolic intermediates are present (Holmberg and Bulow, 1998; Li et al., 2004). Finally, a thorough assessment of the physiological functions and water status of transformed plants is required in order to demonstrate that a transgenic crop is extra-resilient to drought as compared to wild plant species. This will prevent unclear elucidations of how genes affect plant drought tolerance, like those that are frequently found in the literature. To put it another way, it is necessary to distinguish between the direct and indirect impacts of the added genes (for example, improved confrontation of the photosynthesis machinery, contrasted with the effect on growth of leaf and/or plant, flowering of plants, etc.).

Some of the genes being altered by genetic engineering, which are recognized for reacting to water deficit, encode enzymes related to metabolism (e.g., osmotic response or purification), while additional are involved in signal cascade, or transport of metabolites (e.g., transporter of proline), or regulation of energy level in plants. Certain genes, like those that encode the LEA proteins, have no known function but protect the cellular machinery from a variety of stress conditions (Hu, 2008; Huang et al., 2018; Trono and Pecchioni, 2022; Nakashima et al., 2025).

Genetic engineering for water transporters

Both the apoplastic and symplastic pathways are used by plants to transfer water. This implies that many water molecules must pass through a large number of cell membranes. Membrane-intrinsic proteins, the aquaporins, present in all living things that form water-permeable complexes, aid in this process (Uehlein et al., 2003). Aquaporins' phosphorylation state is influenced by the apoplastic water potential, which means that when they are phosphorylated, their capacity to transport water rises. Accordingly, aquaporins are probably going to be crucial in regulating the water status of cells in response to water shortages (Gill et al., 2021; Byrt et al., 2023). It has been demonstrated that distinct physiological activities, such as stomatal opening, are linked to the genes' different expressions of encoding distinct isoforms of aquaporins throughout the development and growth of plants (Chrispeels and Agre, 1994; Gill et al., 2021). It is yet unknown, though, how the gene expression of aquaporins is being regulated and how the aquaporins function in controlling plant water status are related (Aharon et al., 2003). The overexpression of the *Arabidopsis* aquaporin AthH2, which encodes PIP1b aquaporin, in tobacco, for instance, enhanced growing performance in non-stressful situations; nevertheless was ineffective in salt or drought stress (Aharon et al., 2003; Luo et al., 2025).

Aquaporins exhibit cytosolic pH-dependent pathing, which is a change in specific conductance in the water channels, and they can also carry additional minor fragments like ions, solutes, and glycerol, a characteristic that offers a way to coordinately inhibit aquaporins in the plasma membrane when cytosolic acidosis occurs. It was discovered, NtAQP1, a tobacco aquaporin, functions as a protein that facilitates the transport of CO_2 and is important for both opening of stomata and photosynthesis (Millán et al., 2018). In tobacco, overexpression of NtAQP1 boosted leaf development and membrane permeability for water and CO_2, two characteristics that may affect plant performance during drought. These transgenic plants showed an 81% increase in photosynthesis at elevated CO_2 (810 ppm) and a 36% increase under ambient CO_2 (380 ppm). In both cases, stomatal conductance increased in tandem with this (Groszmann et al., 2017; Sun et al., 2024). Thus, the increased mesophyll conductance and additional exposed stomata due to the reduced membrane confrontation to CO_2 may be the cause of the increase in photosynthesis. The cells' availability of CO_2 increased as a result of these actions.

Genetic engineering for C_4 traits in plants

Plant life depends on the capacity to maximise net carbon acquisition and, thus, raises WUE in the presence of decreased water supply (Batool et al., 2024; Gui et al., 2024). High photosynthetic rates in species that use C_4 photosynthetic machinery may be linked to reduced stomatal conductance, which raises WUE (Chaves and Oliveira, 2004). Because it involves coordinated adjustments to stomatal aperture and photosynthesis, manipulating WUE is a very complex desired outcome. After numerous attempts to create C_3–C_4 hybrids by traditional crossbreeding, a number of organizations have effectively converted C_3 plants to obtain C_4 traits (Niklaus and Kelly, 2018; Haghpanah et al., 2024). In a study, researchers have introduced the maize PEPC (phosphoenolpyruvate carboxylase) into rice (Shen et al., 2015), resulting in a greater level of PEPC protein expression (1–3 times greater than leaves of maize). In contrast to C_3 plants, which might achieve 40% of their possible photosynthesis, the altered plants of rice showed a decrease in O_2 blockage during the photosynthesis process, even if no discernible changes were seen in photosynthetic rates (Shen et al., 2015). Theoretically, these transgenic plants might be somewhat superior to the wild kind, particularly under low CO_2 environments, which are common, for instance, during water shortages, when photorespiration-induced carbon loss reaches its maximum. Under supra-optimal temperatures, transgenic potatoes and tobacco showed some positive impacts from the introduction of PEPC (Cui, 2021). According to the concept behind this reaction, PEPC either contributes to the early fixation of CO_2 or raises CO_2 levels near Rubisco.

Another study, grounded on a modelling practice, proposes that C_4 photosynthesis in a solitary C_3 cell may help with the CO_2-diffusion constraints of leaves of C_3 plants, despite being theoretically incompetent because C_4 plants lack the necessary structural characteristics (Leegood, 2002). Once more, this might be advantageous in situations where there is a shortage of water, as stomata close and intercellular CO_2 sharply drops.

Another way to raise WUE would be to increase the catalytic rate of Rubisco or express enhanced versions of the enzyme that have an advanced comparative specificity for CO_2 than for O_2, as those found in rhodophyte algae, to increase photosynthesis capability in C_3 agricultural plants (Carmo-Silva and Salvucci, 2013). Additionally, Rubisco activase, which appears to be more vulnerable to harsh conditions, such as high temperatures, may be overexpressed (Crafts-Brandner and Law, 2000).

Conclusion

The majority of terrestrial plants have evolved to either avoid water deficit by creating methods that preserve water or maximize its attainment, or to escape drought by adopting suitable phenology (**Figure 1**). This demands various signaling methods and early warning systems. Generally speaking, plants must also manage the interplay of additional stresses that frequently occur with dryness and ultimately include oxidative damage. To keep the photosynthetic machinery from suffering irreparable damage, defensive reactions at the leaf level should then be promptly activated in reply to stress molecules. Signals are therefore important for plants' ability to resist stress. Redox signals are increasingly recognized as early warning systems that manage a leaf's energy balance (**Figure 2**). The phenotype, which appears due to numerous genes expression, associated with metabolic pathways and the mechanism of photosynthesis, is regulated by changes in the oxidation-reduction condition of redox-active substances. Additionally, the interaction of many signaling pathways is recognized to be the source of plant responses to stress. The significance of long-distance signaling, that is, the function of chemical signaling produced in roots and delivered to the plant shoot by sap of xylem for the feed-forward reaction of the plant to drought, is recognized. Innovative management strategies that take advantage of long-distance signaling in plants are being used more and more to optimize plant trade-offs between water use and carbon absorption, maintain crop output, and enhance crop product quality. On the other hand, genetic engineering to introduce drought-tolerance traits, also known as "drying without dying" might be a solution for peripheral surroundings, supplementing upbringing efforts and marker-assisted selection for adaptation that investigates the ordinary allelic difference at heritably distinguishable loci. Furthermore, plants may be screened for genes crucial to stress response using QTL mapping in conjunction with relative charting and map-based cloning. Engineering tolerance to various stresses may be aided by a molecular consideration of pressure sensing, transcriptional maintenance, and signaling crosstalk of multiple genes. A solitary gene, for example, a Group 3 *LEA* gene, specifically, which affects the metabolism of sugars, or one that functions as an antioxidant, can be engineered to change metabolism; however, most of the time, this only results in a slight improvement in stress. Recent developments, however, indicate that quick advancements will soon be feasible. Using gene pyramiding or co-transformation, it might be feasible to successfully develop many tolerance responses for single or more abiotic challenges for profitable usage. Furthermore, tolerance may be more reliably provided by upstream targeting of regulatory networks, either through repair or protective mechanisms. Numerous opportunities regarding controlling genes that could be utilized in agronomic agendas to guarantee both endurance in the case of drought and a reasonable level of productivity in the event of reduced water availability are being raised by developments in molecular science for resistance responses in tolerant species.

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This study does not involve human/animal subjects, and thus no ethical approval is required.

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Since this is a review article, so it does not involve any experimentation or use of any types of materials/chemicals.

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The authors declare no conflict of interest.

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