Review Article

Biochemical and Molecular Insights into Abiotic Stress Tolerance in Plants

ABSTRACT

Abiotic stressors, such as drought, salinity, and severe temperatures, must be endured by plants because they are unable to move. Crop yield is reduced by a significant amount due to the effects of these stresses. Molecular mechanisms underlying plant responses to abiotic stress have recently advanced in our understanding, and this new knowledge emphasizes the multilevel nature of these mechanisms, which include multiple processes such as sensory inputs, signalling, transcription and transcript processing, as well as protein translation and modifications after translation. Crop production and agricultural sustainability can be enhanced through genetic, chemical, and microbiological techniques, all of which can be aided by this new found understanding.

Keywords: Stress sensing; ROS signalling; protein phosphorylation; signal transduction; transcriptional regulation; epigenetic regulation; microRNAs; splicing

1. INTODUCTION

Solar energy, CO2, and O2 are all utilized by plants to sustain the Earth's environment by absorbing CO2 and producing O2 and organic matter. Plants distribution and productivity are mostly governed by abiotic factors, which are non-living elements of the environment. Drought, heat, cold, nutrient shortage, high salt, and toxic metal levels in the soil are all constant threats to plants in nature. These abiotic stressors are limiting the amount of agricultural land available around the world, which has a negative influence on crop output [1]. A deeper understanding of the mechanisms by which plants adapt so cope with environmental stress is essential for global food security.

Plants have developed interlinked regulated mechanisms that allow plants to adapt and respond to the environments quickly in order to withstand environmental obstacles. Abiotic stress has a profound impact on plant physiology, inducing wide-ranging alteration in cellular activities. Only a few of the changes are non-adaptive responses that merely reflect stressor induced injury, such as the detrimental changes in membrane fluidity and protein structure caused by heat or cold stress, as well as the disruption of enzyme kinetics and molecular interactions caused by toxic ions in the environment. Alternatively, many of the modifications are adaptive reactions that result in greater stress tolerance, making them suitable crop development targets for breeding. Aspects of the adaptive response include the healing of stress-induced damage, the restoration of cellular homeostasis, and the modification of growth to levels that are appropriate for the particular stress condition [2,3].

Biological responses to abiotic stress are complicated, as proven by genetic, physiological,biochemical, and molecular research (Ref). They include stress detection and signal transmission, transcription and transcription processing, translation, and post-translational protein modifications, among other things. A variety of cell structures and processes, including the cell wall, plasma membrane, cytoplasm and nucleus, as well as chloroplasts, mitochondria, the endoplasmic reticulum and peroxisomes, can initiate these processes [3]. While certain stress-related reactions are universal (for example, the detoxification of excessive reactive oxygen species (ROS)), others are specific to a particular stressor [4-8].

The purpose of this Review is to summarize our present understanding of the components and processes involved at different levels of the molecular response to abiotic stress. We emphasize the characteristics that are similar to those of other stressors. Precision genome editing as well as other methods of improving crop production are now being discussed.

2. STRESS SENSING

A plant's stress response is triggered when environmental stimuli physically or chemically alter the biomolecules within the cell. Because it's difficult to prove that a biomolecule feels stress directly, most potential stress detectors have been discovered in indirect ways+ [9,10]. Secondary messengers including as Ca2+, ROS, nitric oxide, and phospholipids are expected to be affected when sensors are disrupted, and to find the mutations that cause these disorders, genomic screens have been created [11].

2.1 Sensing changes in osmolarity

Plant cells are subjected to hyperosmotic stress due to both drought and salinity. The hyperosmolarity-gated Ca2+ channel OSCA1 in *Arabidopsis thaliana* was revealed as a putative stress sensor as a result of a calcium imaging-based genetic screen in the plant [12]. A decrease in Ca2+ influx into guard cells and root cells, as well as insufficient leaf transpiration, can occur in plants that are subjected to hyperosmotic stress due to an OSCA1 dysfunction [13]. The reduced turgor pressure in hyperosmotic conditions, according to structural analyses of OSCA1 family members in rice and *Arabidopsis thaliana*, reduces membrane tension, which permits the OSCA ion channels to open and Ca2+ to enter the cell, allowing the cell to respond to changes in Ph [14,15]. Comparisons between latent and hyperosmolarity-activated channels could provide evidence for this viewpoint.

2.2 Sensing changes in salinity

Hyperosmotic and ionic stress are present in plants raised in salty soils [14,16]. MOCA1 is the gene that encodes the enzyme that includes a negatively charged glucuronic acid (GlcA) to the plasma membrane's inositol phosphorylceramide (IPC) in response to Na+, and this enzyme has been discovered as a genetic cause of plants lacking in Na+-induced Ca2+ spikes [12,17]. A depolarization of the cell membrane is caused by the binding of Na+ cations to sphingolipids produced by this process. This process has been hypothesized to be defective in moca1 mutant plants due to the fact that GIPC monitors changes in Na+ concentrations in the environment and generates salt-dependent intracellular Ca2+ spikes via an unknown Ca2+ transporter [18]. Both the Ca2+-permeable transporters AtANN1 and AtANN4 have been identified as possible candidates for Ca2+ transport. An electrophysiological and luminescent analysis of root epidermal cells revealed that AtANN1 is required for the generation of Sodium Chloride-activated Ca2+ influx currents in the plasma membrane of the cells [8,18,19]. Mutations in AtANN4, SOS2, and the SOS3-like Ca2+-binding protein SCaBP8 alter *A. thaliana* salt stress-induced Ca2+ signature [20-23]. Phosphorylation of AtANN4 by SOS2 and SCaBP8 forms a negative feedback loop that modifies the Ca2+ signal, resulting in increased Ca2+ uptake [7,25,26]. In order to find out if AtANN1 and AtANN4 have any relation to the MOCA1-dependent GIPC levels, further research is needed.

2.3 Sensing changes in temperature

It is possible that heat and cold stress will have an impact on the fluidity of phospholipid membranes. When plants are exposed to cold stress, their phenotypic abnormalities are caused by the inability of plasma membrane-localized Ca2+ channels or Ca2+ channel regulators to function properly [27,28]. This has resulted in the development of multiple potential cold stress sensors [17,29]. Membrane-localized proteins like the CNGC ion channels may be able to sense alterations in cellular membrane physical characteristics [24,30]. As a result, rice plants with loss-of-function mutations in the genes OsCNGC9, OsCNGC14, and OsCN16 are less tolerant to heat (OsCNGC14) and cold (OsCNGC16) stress than their nonmutated counterparts [31-34].

All cellular compartments can be affected by temperature stress, as evidenced by changes in protein stability and a brief increase in cytosolic free calcium concentration under high temperature conditions [22,23,35]. Under cold stress, the interaction of CBF transcription factors with PIF3, a phytochrome-interacting protein, helps to mitigate the loss of photoreceptor phyB function [15,19,32]. Because PhyB modulates the production of cold-sensitive and growth-related genes, it helps plants to be more resistant to freezing [36,37].

A. thaliana transcriptional repressor ELF3, which regulates numerous growth and development-related genes, senses temperature changes [27,38]. As the temperature rises, ELF3's occupancy of target genes decreases, resulting in an increase in their expression [39].

Although both cold and heat stress can cause changes in cell membrane fluidity and protein conformation, as well as changes in RNA secondary structures, specialized heat shock proteins are able to recognize the buildup of denatured proteins [12,33]. Protein denaturation is only known to occur as a result of heat stress (HSPs). It is believed that these heat stress proteins bind to and inhibit heat stress transcription factors (HSF) in order to prevent the activation of heat-responsive genes and to increase the transcription of other heat stress proteins (HSFs) [40]. Heat stress proteins (HSPs) are released from denatured proteins, which gather and bind to one another to initiate heat stress responses [40,41].

Plants are able to perceive abiotic stressors not just at the cell surface, but also in interior regions like the cytoplasm or nucleus, according to the findings. Direct responses to intracellular conditions may be possible with this capability, as it may allow for compartment-specific response tailoring in response to those conditions.

3. ~~Signal transduction~~ SIGNAL TRANSDUCTION

Stress-specific signal transduction is triggered by the perception of unfavorable environmental situations. In this process, many post-translational modifications (PTMs) of proteins, including ubiquitination, dephosphorylation, oxidation, nitrosylation~~, sumoylation,~~ and sumoylation, are all implicated, among others (ref). Ubiquitination is a post-translational modification that occurs after proteins are translated. ROS and Ca2+, two of the second messengers, are unique in that they play a role in both intracellular and long-distance ~~signalling~~ signaling~~. Signalling~~ Signaling proteins, such as sensors, receptors, and other PTMs, are regulated by PTMs that affect their activity, location, or stability (ref as (5, 6))..

3.1 Ca2+ ~~signalling~~ signaling (as in the figure 1)

Because they are generated by the plasma membrane and organellar membranes in response to stress, these Ca2+ spikes have cell type - and stress-specific timing, intensity, and frequency characteristics; in addition, these Ca2+ spikes have cytosolic and organelle-specific signatures in terms of timing, intensity, and frequency [42-45]. SOS in *Arabidopsis thaliana* recognizes a unique Ca2+ signal, which results in the export of Na+ from root epidermal cells into the soil and the transfer of Na+ from xylem parenchyma cells to xylem vessels for long-distance transmission of Na+ to the leaves [46,47]. Interacting with and activating SOS2, a protein belonging to the SnRK3 family of kinases, in the SOS pathway, which is triggered by SOS2, SOS3 (an EF-hand Ca2+ binding protein) or SCaBP8 is important (also known as the CIPKs) in plants, there are multiple SCaBP/CBL-CPIK complexes that have been discovered [40,48,49]. Complexes such as the SOS3–SOS2 module play critical roles in the Ca2+-mediated responses to diverse abiotic stressors, such as those requiring the modulation of ion transporter functions [50].

3.2 Protein phosphorylation

Phosphorylation of proteins is a critical stage in the transmission of signals during plant responses to various abiotic stress situations. *A. thaliana* and crops such as rice and maize have been proven to be key participants in various stress signalling pathways, with the type 2C protein phosphatase family and SnRK2 protein kinase subfamily being the most well-studied of the two [44,51,52]. In addition to the plasma membrane anion channel SLAC1, which regulates stomatal closure, transcription factors also regulate the plasma membrane NADPH oxidase RbohF, which produces extracellular hydrogen peroxide in the absence of a transcription factor (H_2O_2) [53]. ABA, a phytohormone, is responsible for the closure of stomata in plants in response to hyperosmotic stimuli such as salt, drought, and other environmental conditions, among others [54,55]. In order to limit the function of clade A P2Cs, such as ABI1 and ABI2, ABA receptor proteins (the PYR/PYL/RCAR family of tiny soluble proteins) connect with and physically engage with them [56-60]. Because of this, a number of SnRK2s are liberated from their inhibition by the PP2Cs, allowing them to function normally. However, ABA is not required for the activation of all SnRK2s [61,62]. As an example, cold stress activates both a SnRK2.6/OST1 and a MAP3K-activated SnRK2 independently of either ABA or MAP3K, and both of these RAF-activated SnRK2 families can then phosphorylate inactivated SnRK2 proteins, which in turn can enhance the effects of both the stress and ABA on other SnRK2s that have not yet been activated [63-67]. Ca2+ signalling has been linked to the SnRK3 family, however it isn't apparent how SnRK2s are linked to this process.

3.3 ROS ~~signalling~~ signaling

During abiotic stress, plants create reactive oxygen species (ROS), which include superoxide anion (SOA), hydrogen peroxide (H_2O_2), hydroxyl radical (OH), and singlet oxygen (SO) [68-71]. Stress signalling pathways such as high light stress-induced retrograde signalling (which originates in the chloroplast and travels to the nucleus) and ABA ~~signalling~~ signaling become critical when ROS levels exceed the capacity of the cell to detoxify them [72-75]. The NADPH oxidases RbohD and RbohF are activated by SnRK2, which regulates the generation of H_2O_2 [76,77].

3.4 Systemic ~~signalling~~signaling

Excessive light and water deprivation can lead to systemic acquired acclimation in plants, which is induced by the central nervous system's stress response (CNS) [78-80]. *A. thaliana* distal leaves are protected against extremely high light stress when systemic acquired acclimation (SAA) is activated, which is lethal to non-primed plants unless the system is primed [81,82]. Long-distance electrical and hydraulic impulses are also part of systemic signalling [83]. The vascular bundle RbohD is required for the creation of ROS waves, whereas the vacuolar Ca2+ channel TPC1 is required for the formation of Ca2+ waves [84-88]. It is possible for waves of both types to travel at speeds in excess of one millimetre per second [74,89,90]. As a result of stress, ABA and auxin are transported from the leaves to the roots, where they work together to modify root structure and increase water uptake [66,91-93].

4. TRANSCRIPTIONAL REGULATION

SOS1 transport and guard cell water loss are two examples of rapid adjustments that can be made to restore ion and water homeostasis in plants when stress is induced via a signal transduction mechanism [76,94,95]. This is in addition to the rapid adjustments that can be made to restore homeostasis in plants when stress is induced via a signal transduction mechanism. Transcription factors connect stress-specific transcription patterns to upstream ~~signalling~~ signaling [88,96-98].

4.1 ABA-dependent versus ABA-independent responses

When exposed to drought, excessive salinity, or cold stress, the body uses ABA signalling to regulate transcription of hundreds to thousands of genes [99-102]. Despite this, additional signalling pathways activate many stress-responsive genes [103,104]. ABA-independent cold and drought responsive genes have a TACCGACAT dehydration-responsive promoter element (DRE), while ACGTGG/TC is commonly found in the promoter regions of ABA-regulated genes (ABRE) [105-109].

4.2 Early versus late responses

Stress-responsive genes that encode transcriptional factors respond rapidly, but the expression of many other genes changes later in the stress response and is controlled by the transcribing factors that respond early [110-113] (Figure 1a). CBFs regulate a large number of cold-regulated (COR) genes in *Arabidopsis thaliana*, and they are activated by cold stress by the transcription factors ICE1 and CAMTA [114,115]. It takes one to three hours for CBFs to become active after the onset of cold stress, but the expression of COR genes reaches a zenith within 24 hours after the onset of cold stress [116-119]. CBFs and COR genes are both at their highest levels at the same time [120]. The ICE1–CBF cold-sensing pathway is shared by a large number of plant taxa [121-123]. Under drought, cold, or extreme salt stress, these proteins in *A. thaliana* perform defensive tasks such as detoxification and synthesis of osmolytes, which help to protect the plant from further damage [124,125]. Besides having the effect of enhancing stress responses, transcriptional control has the potential to have a negative feedback effect [126].

5. TRANSCRIPT PROCESSING

It is critical for plant stress tolerance that RNA processing stages including splicing and capping are carried out. Abiotic stress resistance is significantly disrupted by the malfunction of numerous RNA processing machinery components, while the plant's normal functioning is unaffected under stress-free conditions [127-129]. As a result, in order to produce functional mature transcripts, processing machinery that is capable of handling the high amounts of transcripts generated by some stress-responsive genes is necessary [130-132].

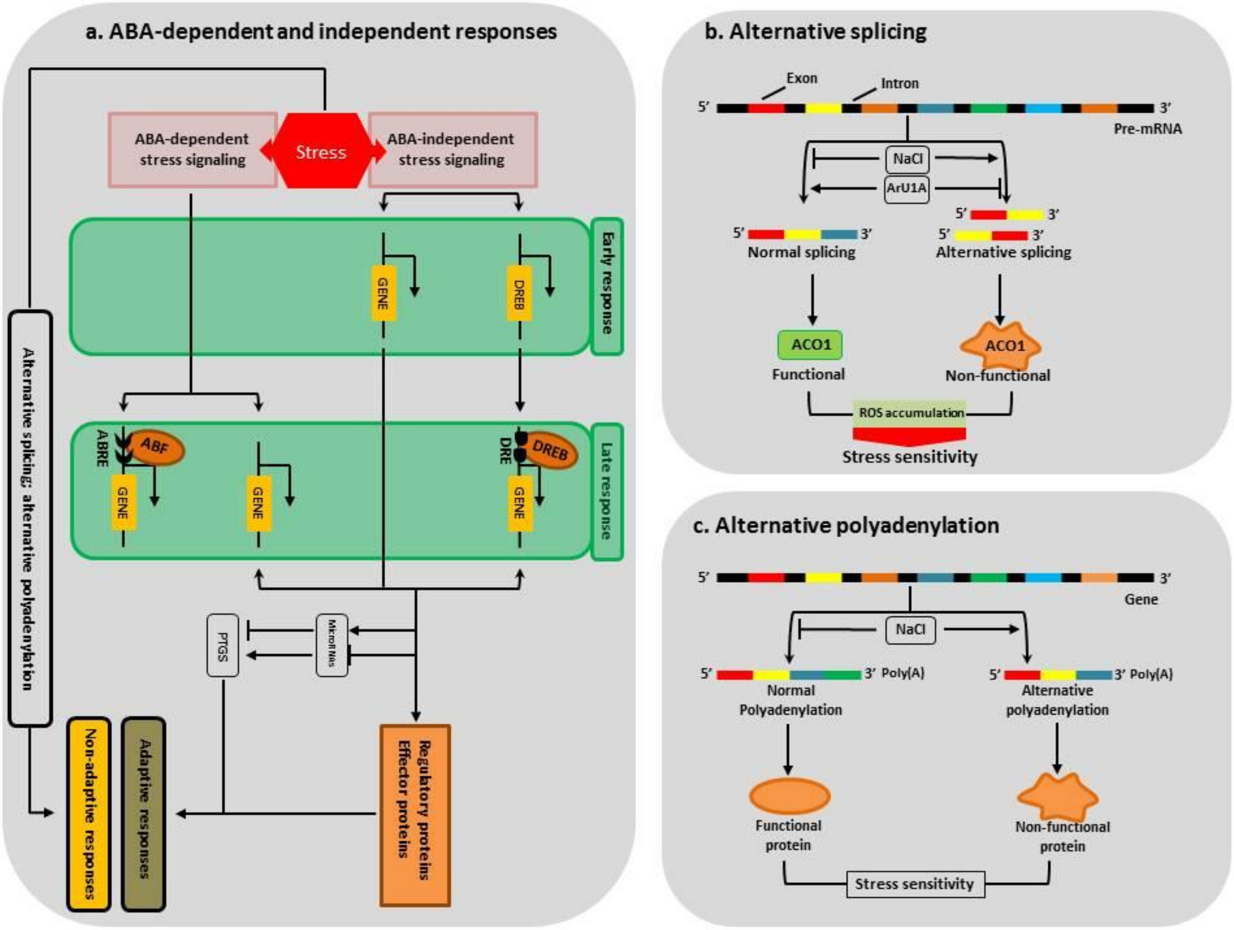

Fig. 1. Stress responses at the levels of transcription and transcript processing

5.1 Stress-induced changes in splicing

The majority of intron-containing plant genes endure alternative splicing furthermore to constitutive splicing, particularly in exposure of plants to cold or salt stress [133,134]. Plant susceptibility to abiotic stress or ABA can be affected by abnormal splicing, which alters the synthesis of functional proteins [135-138]. Splicing in *Arabidopsis thaliana* was disrupted chemically by the macrolide pladienolide B (PB), which has been found to be sensitive to salt, dehydration, and ABA treatment in other plants [139,140] (Figure 1b). While SnRK2 gene expression is unaltered, PP2C gene expression is disrupted, leading to decreased quantities of functional PP2C proteins, which in turn increases ABA signalling [141] (Figure 1b). Hypersensitivity to ABA is caused by errors in the splicing of HAB1 pre-mRNAs in *A. thaliana*, which code for the P2C protein of clade A [142-145].

5.2 Stress-induced changes in polyadenylation

Drought, heat, and salt stress all cause alternative polyadenylation [146]. Abiotic stress alters the transcriptome of numerous genes, causing functional transcripts and translation products in sorghum to switch to nonfunctional status [147,148]. Alternate poly(A) sites have been found to be used by *A. thaliana* transcripts that are enriched for roles in ABA signalling when salt stress is applied [149,150] (Figure 1c).

5.3 Stress-induced changes to microRNAs

When plants face stressful situations, they alter their microRNA levels, which control the amount of target mRNAs by either encouraging degradation or translational repression [151-153]. MiR398 is a microRNA that inhibits the transcription of the Cu/Zn superoxide dismutases (CSD1 and CSD2), which are responsible for detoxifying superoxide radicals [154,155]. Many plants species experience miR319 induction as a result of salt stress [156].

6. TRANSLATIONAL REGULATION

At the ribosome level, stress-related reactions have been documented, including 5′-ribosome halting and blocking the beginning stages of the translation process, as well as structural alterations [108,157]. Heat stress causes mRNA degradation in *Arabidopsis thaliana*, which leads in the halt of the 5′ ribosome, which causes transcripts encoding targets of the HSC/HSP70 chaperones being selectively degraded [158,159]. LARP1 is an RNA-binding protein that serves as a cofactor for the exoribonuclease XRN4 and aids in its ability to cleave polysomes in the cytoplasm [160]. According to *A. thaliana* reduced thermotolerance after being exposed to 35°C for an extended period of time, mRNA degradation is required for plant adaptation and survival under chronic heat stress [56,161]. XRN4 is a transcription factor that regulates the mRNA degradation of HSFA2 (a crucial regulator of plant heat stress responses), and it is absent in plants [121,162]. Atxrn4 gene activity were better able to withstand short-term severe heat stress (43.5°C) than plants with Atxrn4 gene function [163,164]. Host protein HSP101, a chaperone protein that is essential for the release and degradation of mRNAs that have been degraded during heat stress, is required for a rapid resumption of translation once the stress has passed (also known as CLPB1) [134,165].

7. POST-TRANSLATIONAL REGULATION

Many PTMs, which regulate protein localization, accumulation, and/or function, are profoundly impacted by abiotic stress, and this has implications for stress response regulation [140,166]. Prior signalling proteins (such as sensors and receptors) have PTMs (including phosphorylation, as stated above) that allow them to respond immediately to stress, but It is possible that PTMs on freshly synthesized proteins as a result of stress-induced transcription are also essential [167].

7.1 Stress-induced post-translational modifications of other proteins

PTMs are responsible for the regulation of a number of stress-resistance-enhancing non-signalling proteins [168,169]. A variety of enzymes, including those involved in ROS generation and scavenging, as well as those involved in the manufacture of osmolytes, are phosphorylated by SnRK2s when they are triggered by osmotic stress and the ABA signal [170].

8. EPIGENETIC REGULATION

Epigenetic markers influence the expression of genes associated with stress response and stress tolerance [141,171]. Histone modifications and DNA methylation are responsible for the structure of chromatin as well as the accessibility of DNA for transcriptional activity [140,172-175]. Many plant species have had their epigenetic marks altered in response to a variety of abiotic stress treatments, and these differences have been linked to the transcriptional control of genes implicated in plant stress responses [176].

Changes in epigenetic regulators can also cause stress-induced changes in plant epigenetic patterns [177]. Researchers believe that the flavor of tomato (*Solanum lycopersicum*) fruits degrades because cold treatment impedes transcription of the DNA demethylase gene DML2, allowing a rise of DNA methylation in genes involved in biosynthesis of aromatic flavors, which then causes the expression of those genes to be silenced, resulting in the flavor of tomato fruits degrading [143,178].

8.1 Erasure of stress-induced epigenetic changes

An epigenetic alteration resulting from abiotic stress may lead to transgenerational stress memory [179]. During stress recovery, however, mechanisms exist to reverse stress-induced epigenetic changes [156,180]. Epigenetic gene silencing in *A. thaliana* is mediated by two different proteins: the chromatin remodeling protein DDM1 and the DNA helicase MOM1 [167,181]. DDM1 works through DNA methylation, while MOM1 does not. Plants that lack both MOM1 and DDM1 are not able to pass on heat stress-induced epigenetic silencing to their progeny, suggesting that both of these proteins are necessary to prevent stress-induced epigenetic inheritance [182,183].

9. IMPLICATIONS FOR CROP IMPROVEMENT

We currently know a lot more about how plants respond to abiotic stress because to studies on the *thaliana* species. *A. thaliana* general principles may be applied to crops, but their underlying molecular details are often somewhat different. *A. thaliana* and crop gene homologues typically do not have a perfect one-to-one correspondence because of genetic variation in protein complexes and spatial and temporal expression levels [184]. This is owing to the fact that the vast majority of plant genes are organized into families. Although more understanding of the genes and pathways involved in *A. thaliana* is required for informative biotechnological agricultural production, it can also help in the creation and analysis of natural genetic variation, which may prove to be a valuable commodity in the future when breeding stress-resistant crops.

The identification of the essential regulators of abiotic stress tolerance and spontaneous allelic variants in crop species has been made possible in recent years through the use of quantitative trait locus methods and genome-wide association analysis [185]. It is possible that the genes and alleles uncovered by these techniques will be useful for breeding crops that are more resistant to environmental stress while also producing higher yields. Several HKT1 alleles in rice, wheat (*Triticum aestivum*), and maize (*Zea mays*) have been identified as critical quantitative trait loci regulating plant salt tolerance, paving the way for marker-assisted breeding of wheat to produce higher yields in salinity-saturated soil [186].

9.1 Genetic engineering of stress-resilient plants

Through the use of genetic engineering techniques, it is feasible to develop stress-resilient plants by altering the expression or activity of critical regulators associated with stress responses [139,187]. Although regulators at any level of the molecular response can be altered, protein kinases, and other signalling factors, transcription factors, metabolic enzymes, as well as ion transporters, have shown to be the most successful targets for genetic alteration [188]. Plants grown in transgenic rice that express the stress-inducible gene OsDREB2A showed higher tolerance to dehydration stress than plants produced in transgenic rice that did not express the gene [154,189]. Stress circumstances frequently result in an excess of the lethal metabolite methylglyoxal being produced in the body (MG) [98,190]. Abiotic stressors such as high salt concentrations, dry conditions, and high temperatures were made tolerable by increasing the expression of genes related with the glyoxalase pathway for MG detoxification in *Oryza* species [191]. Through the use of a short tandem target mimic method to knock down miR166 in rice, researchers were able to induce increased drought tolerance and developmental alterations that were similar to natural plant responses to water scarcity stress [67,192]. In order to develop alleles with increased or decreased stress response expression, it is possible to incorporate transcriptional or translational regulatory sequences into key stress response genes. This technique is particularly useful for both research and breeding because it allows for the development of alleles with increased or decreased stress response expression.

9.2 Increasing stress resilience without sacrificing growth

There is a strong relationship between plant stress responses and other key biological processes, particularly growth-related pathways in plants. Due to the negative side effect of reduced growth, increased crop stress resistance is often accompanied with a fall in yields [193]. Through the expression of stress tolerance genes, stress-inducible promoters can help to reduce these growth and yield penalties. Better frost tolerance was seen in transgenic wheat and barley (*Hordeum vulgare*) that had constitutive overexpression of TaDREB2 and TaDREB3, but growth and blooming were significantly delayed [194]. Drought-inducible promoters induced the expression of TaDREB2 and TaDREB3 in transgenic wheat and barley plants, resulting in increased drought survival [195]. However, when the plants were not stressed, no abnormal growth was seen. In a similar vein, drought-induced Oshox24 promoter-controlled overexpression of the transcription factor gene OsNAC6 boosted rice tolerance to dehydration and severe saline stress without producing growth retardation or low grain production in the field [196]. Stress reactions and plant development have an antagonistic relationship, as demonstrated by the reciprocal regulation of PYL proteins and the TOR kinase. This means that the two processes are in a state of well-regulated equilibrium with one another [125,197].

9.3 Chemical intervention to protect plants from abiotic stress

Small-molecule chemical compounds that modify the activity of molecular components in plant stress response networks have the potential to control these networks. In the field, ABA therapies are not frequently employed due to the high cost and chemical instability of the treatments, despite the fact that they have the ability to protect plants from a wide range of abiotic hazards. The identification of ABA receptors and the architecture of these receptors has aided in the development of ABA mimics [198]. Researchers are investigating the effects of these small molecules, which are capable of binding to ABA receptors while also triggering stomatal closure and increasing the synthesis of stress-responsive genes [199,200].

10. CONCLUSION AND FUTURE PROSPECTS

Scientists are still confused by plant molecular responses to abiotic stress, particularly in the areas of stress detection, early ~~signalling~~ signaling, translational and post-translational control, and growth regulation, among other areas. These presumptuous stress sensors are likely to be many, but their physiological roles and biochemical detection procedures remain unclear, therefore they can only be referred to as presumptive stress sensors.

The majority of known stress ~~signalling~~ signaling pathways have not been linked to stress sensors, crosstalk across ~~signalling~~ signaling pathways is not fully understood, and ~~signalling~~ signaling networks are still in the process of being established. The application of numerous distinct omics approaches has significantly enhanced our current understanding of molecular genetics. Because of genetic redundancy and lethality, as well as a limited ability to analyse biologically huge amounts of data, unravelling plant stress response pathways and regulatory networks presents significant obstacles.

Given our limited understanding of plant stress responses, it is possible that even a combination of genetic and pharmacological techniques will not be sufficient to protect plants against stress in the field. Microbes may be able to provide a solution to this dilemma. The rhizosphere is a microenvironment where plants and soil microorganisms dwell. It is the makeup of the root microbiota that is highly influenced by a plant's genotype and environmental stressors, and it is at this point that root exudates play an important role [201].

Several different abiotic stresses are applied to plants at the same time in their natural environment, thus it is critical to understand how different types of stress affect the body's response system in different ways. Plant responses to biotic and abiotic stimuli such as ROS generation and stomatal closure are two examples of plant responses that may converge at certain regulatory nodes in response to biotic and abiotic stimuli. This interplay of reactions and their cross-talk has the potential to have either synergistic or antagonistic effects, resulting in either increased or decreased stress levels resistance. It will be necessary to discover the molecular mechanisms by which plants respond to a wide range of environmental stresses in order to generate stress-resistant crops in the field.

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