Plant RNA-binding proteins as key players in abiotic stress physiology

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ABSTRACT

Abiotic stress has a major effect on global crop production. Hence, plants have evolved and developed several response mechanisms to survive and grow under abiotic stresses. Plant cells can sense and respond to changes in different environmental stresses due to the specific modifications observed in gene expression, metabolism, and physiology. Only a few recognized sensors have been found due to the difficulty of functional redundancy in genes that code for sensor proteins. A defect in one gene causes no remarkable phenotypic changes in stress responses. Recent research has identified crucial RNA-binding proteins (RBPs) important for stimulus-specific responses. RBPs play a crucial part in plants' growth and development, post-transcriptional gene regulation, and RNA metabolism induced during stress responses. Among the currently identified over 200 different RBPs, the majority of which are plant-specific and carry out plant-specific functions. As an essential component of plants' adaptive process in different environmental conditions, RBPs regulate the following processes: RNA stability, RNA export, pre-mRNA splicing, polyadenylation, and chromatin modification. Plants have also developed different defense responses or molecular mechanisms to combat stress *via* genotypic and phenotypic expressions. With a unique understanding of RBPs in other organisms, RBPs functions in a plant are still limited. Hence, this review discusses the latest developments in RBPs function during the development and growth of plants, primarily under abiotic stress circumstances.

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1 Introduction

Plants are immobile organisms that adapt to various physiological changes and environmental stresses. Stress can be biotic and abiotic, which impacts plant productivity and fertility. Global warming and increased plant productivity are impacting the global population where agricultural products are being threatened by several factors such as temperature, precipitation changes due to climate change, and increasing concentrations of atmospheric carbon dioxide (CO_2) (Zhao et al. 2017; Singh and Thakur 2018). Abiotic stress like pH, temperature, salinity, drought, and climate change challenge the growth and development of plants (Singh and Thakur 2018; Dresselhaus and Hückelhoven 2018). Drought and salinity are considered major abiotic stresses that minimize plant productivity and challenge global food security (Munns et al. 2020; Téllez et al. 2020). These two stressors raise ion toxicity, oxidative stress, evapotranspiration, water, and nutrient deficiencies in plants (Téllez et al. 2020). Thus, developing stress-resistant plants is among the most significant challenges in agrobiotechnology research (Dresselhaus and Hückelhoven 2018).

Combating the abiotic stress requires analyzing the plant's functional metabolites with translational research and enhances resources for genetic studies. Increasing the limited gene pool of wild-type plants and conducting extensive molecular studies with the omics approach is essential. These studies will clarify the mechanisms underlying abiotic stress and their responses. Various translational approaches with next-generation sequencing, transcriptomics, metabolomics, and reprogramming techniques are used to enable the plants to overcome or tolerate abiotic stresses. Also, further knowledge of plant stress physiology and its complexities is explored by developing innovative computational tools (Dresselhaus and Hückelhoven 2018).

Gene expression and its regulation occur at transcriptional and post-transcriptional levels, which is critical for plant growth and development. Plant response and adaptation to different external stimuli depend specifically on post-transcriptional regulation. Regulation of RNA metabolism, among others, is an essential modification that involves RNA-binding proteins (RBPs) directly or indirectly (Lee and Kang 2016). Research is focused on elucidating the molecular mechanisms underlying stress responses. Plants have diversified RBPs in different cellular and physiological processes. Translational investigations on RBPs and RNA-protein interactions have been done that led to the identification of numerous conserved protein motifs and domains in organisms, including plants. These conserved portions are RNA-recognition motifs (RRMs), zinc-finger motifs, K-homology domain (KH), arginine- and glycine-rich domains, and SR repeats (Jung et al. 2013). RBPs are widely recognized as functional modulators in major abiotic stresses involving the ones mentioned earlier (Marondedze 2020). To deal with abiotic stress, plants reprogrammed their gene expression rapidly, which requires transcriptional and post-transcriptional modifications. An essential molecular response by plants with an increased focus on post-transcriptional gene regulation along with RNA granules' discovery as stress granules have led to the recognition of crucial RBPs due to environmental stresses (Yan et al. 2022).

The identification of several plant RBPs is essential for stimulus-specific responses. Plants can also respond against abiotic stress stimuli because of these RBPs. They are now widely acknowledged as a regulating element of post-transcriptional gene expression (Marondedze et al. 2019). The binding of RBPs to mRNA occurs *via* RNA-binding domains (RBDs). This binding determines the amount of RNA accessible for translation, stability, turnover, and other critical elements for stimulus-specific responses (Marondedze et al. 2019). External conditions resulting from sudden environmental changes, such as climatic changes, salinity, temperature, pH, and desertification, significantly affecting plant growth, development, and productivity, is the main focus of this review.

Numerous abiotic stresses like high temperature, salinity, drought, heavy metals, submergence, and nutrient insufficiencies harm a plant's development and growth. This is attributable to the emerging ecological effects of climate change on plant growth and development (Bellard et al. 2012). These ravaging effects of climate change (abiotic stresses) have thus initiated research on developing climate change-resilient plants (Rosenzweig et al. 2014). Hence, this review discusses the latest developments in RBPs function during a plant's development and growth, primarily in abiotic stress conditions.

2 Plant Stress Physiology and its repercussions on abiotic stresses

The concept of plant stress introduces the biotic and abiotic stresses which impact plant growth, development, and productivity. The abiotic stresses play an adverse role as the external conditions are the most stressful environments that affect plant growth. Any abiotic stress factor leads to less productivity and affects global food production. Hence, it is imperative to study the various factors that affect plant physiology and how plants respond to these abiotic stress (Shabala and Munns 2017).

Stress response depends on several factors, such as the duration and severity of stress, tissue specification, and genotype of the plant. The physiological responses to abiotic stress may have three possibilities i.e. tolerance, susceptibility, and avoidance (Figure 1). Tolerance mechanisms allow plants to survive either by tolerating or by avoiding stress. The ability to tolerate a particular stress over time made these plants stress-resistant, as they can adjust or acclimate to the stress. The tolerance mechanism also allows for
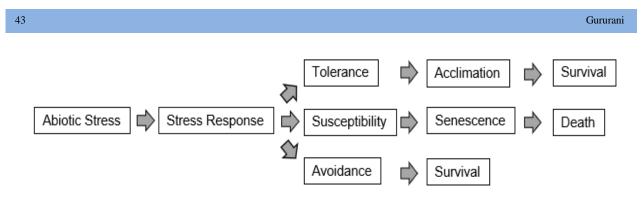
Figure 1 Schematic representation of the effect of environmental stress and plants' response

maintaining of high metabolic activity under moderate stress and reduced metabolic activity under severe stress. But, avoidance reduces metabolic activity during extreme stress, which results in a dormant state (Choudhury et al. 2017; Gururani et al. 2015a). Plants display stress resistance or tolerance because of their genetic ability to acclimate to stress and develop a new state of homeostasis over time.

In plant stress physiology, acclimatization and adaptation are essential. While acclimatization does not require genetic modification but rather changes in plant physiology (phenotypic response) to accommodate shifting environmental conditions, but adaptation takes place at the genetic level where favorable genes that are adapted to stress are acquired over several generations. For example, plants become resistant after prolonged exposure to cold or freezing temperatures over a longer duration by adjusting their growth and metabolism to suit the low temperature.

Numerous biotic and abiotic stresses affect plants that trigger variable plant responses, like altered gene expression, modified growth rates, and cellular metabolism. However, plants have also developed different defense responses or molecular mechanisms to combat these stresses *via* genotypic and phenotypic expressions (Abuqamar et al. 2009). One such mechanism is by reactive oxygen species (ROS)(H_2O_2 and superoxide $\cdot O_2^-$) generated during oxidative stresses that cause major cellular damage (Allan and Fluhr 2001; Bartoli et al. 2013). Hence, plants remove ROS rapidly *via* its anti-oxidative mechanisms it can also be minimized by stress and further tissue damage (Allan and Fluhr 2001; Kimotho et al. 2019). Also, to induce a particular response to environmental and developmental cues, ROS interacts with some other cell signaling pathway components including hormones, RNS, and intracellular Ca^{2+} fluxes (Farooq et al. 2019).

Through the mitogen-activated protein kinase (MAPK) cascades, plants also react to abiotic stress, which is activated by even a mild sense of stress (Wurzinger et al. 2011). These are in charge of signal transduction for a variety of biotic and abiotic stress reactions in many cellular functions. Due to their involvement in various stress responses, MAPKs are crucial in the combined biotic and abiotic stresses (Danquah et al. 2014). Further, hormone signaling is also essential for mitigating biotic and abiotic stress reaction effects. The H_2O_2 signaling involves the MAPK pathway regulating gene expression during defense and hypersensitive responses (Farooq et al. 2019). Among these, the main hormone responsible for the coordinated abiotic stress response in plants is abscisic acid (ABA), by tackling decreased moisture availability in these plants (Figure 2) (Raghavendra et al. 2010; Kimotho et al. 2019). ABA-dependent pathways for gene activation, which influence stress tolerance are achieved by two regulons: the myelocytomatosis oncogene (MYC)/myeloblastosis oncogene (MYB) regulon and the ABA-binding factor/ABA-responsive element binding protein (ABF/AREB) regulon (Saibo et al. 2009). Rapamycin (TOR) is an atypical Ser/Thr protein kinase that regulates energy maintenance and metabolic homeostasis in plant stress responses and adaptation (Fu et al. 2020)

Temperature is a key element in the metabolism and growth of plants. It is shown that rapamycin (TOR) activity in *Arabidopsis* is diminished rapidly by cold stress at different time points and recovers back after 2 hours of treatment. TOR activity is also in extreme temperature tolerances (Fu et al. 2020). Many studies have examined drought and heat stress's effects on plants. According to Nadeem et al. (2018), a plant's growth stages may be impacted by heat stress, and in response, plants evolve defense mechanisms to protect against damage to membranes and control transpiration and photosynthesis. Heat stress induces molecular responses such as NO, ROS, Ca^{2+} signaling pathways, and initiation of heat stress factor (HSFs) genes as well as other transcriptional factors.

Heat stress diminishes the photosynthetic efficiency reducing the plant life cycle and productivity. The major physiological change brought on by heat stress in plants is membrane dysfunction. Heat stress induces kinetic energy, which moves the biomolecules across membranes detaching the chemical bonds. This increases membrane fluidity (Zhao et al. 2020). Additionally, Begcy et al. (2018) stated when Australian and European wheat cultivars are exposed to moderate heat stress, reduced photosynthesis, transpiration rate, and pollen viability are observed in European cultivars (HSFs down-regulated or up-regulated) compared to
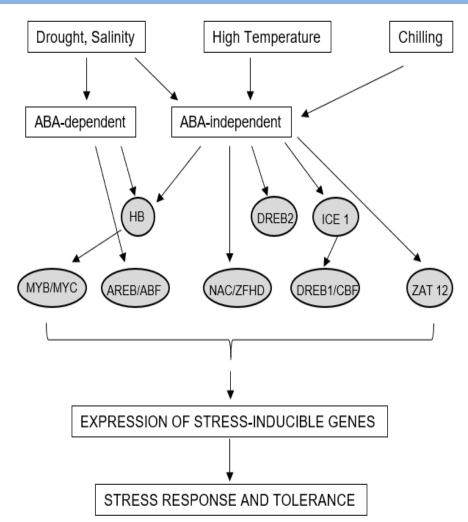
Figure 2 A schematic diagram of the cross-talk network between cis-acting components and transcription factors

Australian cultivars. This shows better adaptation to heat stress in Australian cultivars than the European cultivars. The results of a similar study utilizing wheat cultivars experiencing terminal heat stress conducted in several locations in Egypt demonstrate that heat stress had a significant detrimental effect on plant growth and resulted in nearly 40% less yield (Elbasyoni 2018).

Plant water maintenance is essential for turgor pressure, increased surface tension, and various biochemical processes. Distribution of water throughout the year will ensure proper plant production and yield. But conditions of water stress or drought are frequently unpredictable. Approximately 50% of global loss of crop yield is due to drought stress (Khalid et al. 2019). Drought stress tolerance could be achieved in *Arabidopsis* by restricting transpiration and improving water use efficiency (WUE) (Blankenagel et al. 2018). Their findings also show huge potential for improving WUE in cereals but with reduced assimilation and growth rates. Xiong et al. (2018) used the pak choi plant to study the effects of nitrogen

supply and drought stress. They reported pak choi showing significant and better growth under drought stress when supplied with higher nitrogen concentrations.

Water logging is a major issue, not just in areas with heavy rainfall but also in irrigation water-used areas. In a few nations, flooding has affected 0.7 million acres and 60000 acres are permanently under water from poor drainage and water channel leakage. Water logging circumstances significantly reduce a plant's production and yield when it is still developing. However, the impact is minimal and only noticeable briefly when a plant is dormant. Flooding extensively impacts seed germination, decreases vegetative and reproductive growth and plant structure, and accelerates aging (Khalid et al. 2019).

Methods applied to improve crop resistance against floods have been extensively studied focusing on barley, maize, and soybean (Mustroph 2018). They confirmed the presence of tolerance genes

by identifying various trait loci (QTLs). Using natural salinity stress-tolerant plant quinoa, Messerer et al. (2018) emphasized next-generation sequencing technology (RNA-seq) to uncover stress-related genes, which may lead to higher salt tolerance.

3 Stress Sensing and Signaling

Plant cells can presumably sense and respond to changes in different environmental stresses due to the specific modifications observed in gene expression, metabolism, and physiology. Only a few recognized sensors have been found due to the difficulty of functional redundancy in sensor protein-coding genes. A defect in one gene causes no remarkable phenotypic changes in stress responses.*Arabidopsis* OSCA-1 gene is a potential hyperosmotic stress sensor (Yuan et al. 2014). ABA and osmotic stress factors like cold, heavy metals, heat, high salt content, and oxidative stress may elevate free cytosolic Ca^{2+}ions in plants that can be identified *via* genetically encoded aequorin. The COLD1 stress sensor is another potential sensor that mediates rice's cold stress sensing required for chilling tolerance ($0–15^0$C) in the rice subspecies *Nipponbare* (Ma et al. 2015). Transmembrane protein COLD1 controls calcium channels or senses calcium channels that sense cold as it interacts with RGA1 in plants (Ma et al. 2015). But it is still ambiguous if the chilling tolerance is due to the COLD1-mediated calcium signaling.

The fluidity of cellular membranes is modified by cold and heat stress that could be sensed by various channels, integral membrane proteins, transporters, and membrane-anchored receptor-like kinases (RLKs) (Sangwan et al. 2002). Certain molecular chaperones that bind misfolded proteins can sense the denaturation due to heat stress, which releases related transcription factors from the chaperones to initiate the heat-responsive genes (Scharf et al. 2012).

Plants with many MAP kinase family members assemble to produce many MAP kinase modules. For instance, *Arabidopsis* has 20 MAP kinases (MAPK), 10 MAP2 kinases (MAP2K), and more than 60 MAP3 kinases (MAP3K) (de Zelicourt et al. 2016). The abiotic stresses such as high salinity, drought, heat, cold, and wounds activate MAPKs in plants multiple times (de Zelicourt et al. 2016). Identification of the upstream protein sensors, MAP2Ks, and MAK3Ks, responsible for activating MAPK, and methods of connecting kinase activation to downstream effects on proteins and physiological outputs present the greatest challenges in characterizing MAPK-signaling pathways for abiotic stress (Danquah et al. 2014; de Zelicourt et al. 2016).

A drought-response photoreceptor, phytochrome C1 in *Z. mays*, has been identified for drought sensing in plants, though specific receptors have not been discovered yet (Benešová et al. 2012). Phytochrome is supposed to regulate light-responsive gene transcription by controlling numerous transcription factors' activities for biotic and abiotic stresses (Gururani et al. 2015a). In *Arabidopsis*, 3 phytochrome genes (PHYA, PHYB, and PHYE) suppress drought tolerance, which implies that phytochrome C may mediate osmotic stress (Boggs et al. 2010). Similarly, it has been shown that turf grasses can recover from salinity, heavy metal toxicity, and cold stress when a hyperactive Ser599Ala PHYA from oat is over-expressed (Gururani et al. 2015b; Gururani et al. 2016).

Osmotic regulation is essential for a plant's drought resistance. Under drought stress, various crucial osmotic homeostasis-related proteins, including betaine aldehyde dehydrogenase (BADH), dehydrin (DHN), and late embryogenesis abundant (LEA) protein, are gathered in leaves. LEA proteins have high hydrophilic proteins that aid in stabilizing cellular components due to water loss (Chakrabortee et al. 2007). Similarly, other studies have shown that DHNs (group 2 LEAproteins) have higher hydrophilicity and thermostability, which were extensively drought-accumulated among many plant species such as *Z. mays, T. aestivum*, *C. dactylon,* and *B. napus*. These DHNs stabilize the protein structure *via* detergent-chaperone-like properties (Hu et al. 2010; Jangpromma et al. 2010). Also, DHN in *Z. Mays* has shown a noticeably higher level of phosphorylation under drought stress (Bonhomme et al. 2012). Phosphorylation of LEA2 may increase its calcium binding since it functions as a calcium buffer and has calcium-dependent chaperone-like action similar to that of calreticulin and calnexin (Alsheikh et al. 2003). Group 3 LEA proteins also increase in *Z. Mays* and *B. napus* during specific drought conditions (Benešová et al. 2012; Koh et al. 2015). Studies have demonstrated that the LEA gene provides drought stress resistance in various plant species. For example, transgenic calli over-expressing sweet potato LEA14 (IbLEA14) increased drought stress resistance. In contrast, RNA interference (RNAi) calli showed enhanced drought stress sensitivity (Park et al. 2011). It can be concluded that LEA could be used to enhance plants' drought tolerance.

4 Regulators of Plant's Abiotic Stress Responses

Plants respond to abiotic stresses with various molecular mechanisms, such as cross-talk and interactions between several molecular pathways (Takahashi and Murata 2008; Gururani et al. 2015a). The plant signals involved in abiotic stress responses are reactive nitrogen species (RNS) and reactive oxygen species (ROS) that can alter gene regulation and enzyme activities (Molassiotis and Fotopoulos 2011; Singh and Thakur 2018; Akilan et al. 2019; Varghese et al. 2019). Further, abscisic acid (ABA) and ethylene are the most significant hormonal regulators of plant responses to abiotic stresses (Wilkinson and Davies 2010). ABA regulates osmotic stresses through transcriptional activities by

regulating these plants' ion and water transport processes (Pettigrew et al. 2015). Ethylene is also involved in stress responses such as wounding, drought, flooding, chilling, heat, ozone, and UV-B light (Goda et al. 2008; Stepanova and Alonso 2009; Wilkinson and Davies 2010; Pettigrew et al. 2015). MicroRNAs (miRNAs) have demonstrated abnormal expression induced due to abiotic stress, which implies miRNAs be specific targets for developing genetically modified stress-resilient plants (Banerjee 2020). It is now known that epigenetic mechanisms like histone modifications, DNA methylation, and chromatin remodeling are involved across all abiotic stress responses. Along with such modifications, long non-coding RNAs and small RNAs regulate the abiotic stress response and RNA silencing (Chang et al. 2020).

Similarly, C_2H_2-type zinc finger proteins play a crucial part in the growth of plants, development, and resistance to abiotic stress. Studies on the functional roles of these proteins in different stress-resilient plants like halophytes and xerophytes are being explored to identify certain regulated genes. Rapid advancements in sequencing technologies will help in plants' epigenomic profiling, which may help us study further mechanisms of stress adaptation (Chang et al. 2020).

5 RNA-Binding Protein (RBP)

Ribonucleoprotein (RNP) complexes are produced when RBPs bind to RNAs. These complexes are essential for all aspects of post-transcriptional gene regulation (Glisovic et al. 2008). Currently, more than 1000 RNPs are known that participate in plants' adaptation to various environmental conditions. RBPs are therefore essential for all organisms in regulating cellular physiology and gene expression. A few RBPs have been identified in plants; some of which are involved in the plant's innate immunity and its responses (like GaPR10, tcI14, PRP-BP, GRP7, etc.) (Fedoroff 2002; Woloshen et al. 2011).

5.1 RNA binding domains (RBDs)

According to Lunde et al. (2007), each RBP have a specific RNA binding domain (RBD) to bind on RNA. These RBDs must be able to identify particular RNA sequences (Figure 3). The double-stranded RNA binding domain (ds-RBD), RNA recognition motif (RRM), zinc finger binding domain (ZnF), DEAD box helicase domains and K-homology domain (KHD) are some of the most significant RBDs out of more than 400 already identified ones (Cléry et al. 2008; Valverde et al. 2008; Linder and Jankowsky 2011).

RNA binding is reliant on recognizing RNA structures and specific nucleotide sequences. However, RBPs utilize multiple instances of the same RBD to improve RNA binding affinity and specificity by enhancing the binding space (Lunde et al. 2007). The most frequent RBD in eukaryotes is RRM, found in 0.5–1% of genes (Cléry et al. 2008). Each RRM can recognize only 2-8 nucleotides, but the presence of more RRMs (4 or more) can recognize nucleotides at different sites within the RNA, thus increasing RNA restructuring rates (Sawicka et al. 2008).

RNA binding specificity is enhanced when certain RBPs interact with several types of RBDs (Afroz et al. 2014). The RNA-binding proteome or "RBPome" is essential to cell function, tightly
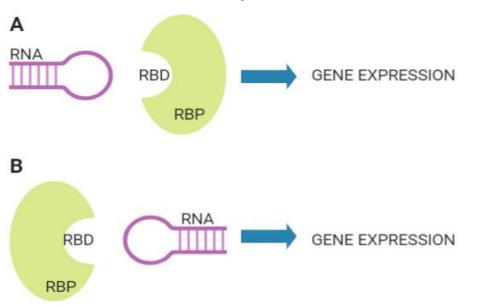

Figure 3 Cross-talk between RNA and proteins: A: RNA and RNA-binding protein (RBP) interact via a defined RNA-binding domain (RBD) and regulate RNA metabolism and functions. B: RNA can interact with RBP and regulate its functions (Adapted from Hentze et al. 2018)

regulated, and shows altered responses with varying environmental changes (Sysoev et al. 2016; Perez-Perri et al. 2018; Garcia-Moreno et al. 2019; Trendel et al. 2019).

A comprehensive strategy involving the RNA interactome capture (RIC) technique exposes ultraviolet (UV) irradiation of cells to enhance RNA-to-protein crosslinks. The RIC approach has enabled the identification of proteins that bind to polyadenylated RNAs in living cells (Baltz et al. 2012; Castello et al. 2013). The RIC approach enables the identification of proteins that are in close contact with RNA, exposes RBPs acting in their natural environment, and can be used in comparative studies to uncover RBP dynamics (Sysoev et al. 2016; Perez-Perri et al. 2018; Garcia-Moreno et al. 2019).

RIC technique has been utilized on different organisms, including *Arabidopsis thaliana* and plant leaves since 2012 (Bunnik et al. 2016; Lueong et al. 2016; Bach-Pages et al. 2017). Only 27 RBPs in the leaf were identified in one study to compare approximately 226–372 RBPs produced in the other plant species (Marondedze et al. 2016; Hentze et al. 2018). It is difficult to apply RIC in plant leaves due to the cell walls, chlorophyll (UV-absorbing pigments), secondary metabolites, and reduced UV-crosslinking efficiency due to leaf thickness (Köster et al. 2020).

Eukaryotic gene expression is regulated at the transcriptional and post-transcriptional levels. At the post-transcriptional level, small nuclear ribonucleoprotein particle (snRNP) proteins, poly(A)-binding proteins (PABPs) for mRNA stability, SR proteins for RNA splicing, heterogeneous nuclear ribonucleoprotein particle (hnRNP) proteins for RNA transport are important regulated proteins (Suzuki et al. 2000). RBP binding to target RNAs is required to regulate RNA metabolism. RBPs consist of several conserved motifs and domains like K-homology (KH) domain, RNA-recognition motif (RRM), zinc finger motif, RD-repeats, glycine/arginine-rich regions, and SR-repeats (Lee and Kang 2016).

6 Role of RNA-Binding Protein in Abiotic Stress Responses

RBPs are remarkably conserved and diverse. RBPs with one or more RNA-binding domains (RBDs) recognize RNA-protein interactions forming ribonucleoprotein complexes (RNPs). RBPs are categorized as cold-shock domain proteins (CSDP), glycine-rich RNA-binding proteins (GR-RBP), zinc finger glycine-rich proteins (RZ), S1 domain-containing proteins (SDP), pentatricopeptide repeat proteins (PPR), DEAD-box RNA helicases (RH), and chloroplast RNA splicing and ribosome maturation domain (CRM). RBPs encompass some classic proteins, such as RBPs with K-homology domain (KH), RNA recognition motif (RRM), and arginine-glycine repeats (RGG) (Lee and Kang 2020). The essential functions of some RBPs in abiotic stress response are discussed below.

6.1 RNA Recognition Motif

RNA recognition motif (RRM) is the best-known RNA binding motif which comprises a maximum of RBPs (Lee and Kang 2016).

6.2 K-homology domain

After RRM, the heterogeneous nuclear ribonucleoprotein K (hnRNP K) homology (KH) domain protein is the RNA-binding domain that is most frequently observed. Every KH domain contains a highly conserved consensus sequence (VIGXXGXXI) at the center of a 60 AA long chain with a typical hydrophobic residue pattern. Proteins can contain several copies of KH domains (up to 15). A protein with a KH domain is capable of binding single-stranded DNA or RNA to control genes' transcriptional and post-transcriptional regulation. By changing numerous genes' expression regulated by abiotic and biotic stimuli, the *Arabidopsis* KH-Domain RNA-Binding Protein ESR1 insertional knockout mutants' esr1-1 and esr1-2 confer enhanced heat tolerance (Muthusamy et al. 2021).

6.3 Cold-shock domain proteins (CSDP)

The cold shock domain (CSD) is found in the eukaryotic Y-box proteins that may bind RNA and single-stranded and double-stranded DNAs. In contrast to bacterial cold shock protein (CSP), which only has the CSD, typical plant CSDPs have CSD at the N-terminus, and at the C-terminus, a glycine-rich region is found that is interspersed with multiple zinc fingers of the CCHC type.

When exposed to cold, *AtCSP2* overexpression markedly reduced freezing tolerance, but the *atcsp2* mutant dramatically increased freezing tolerance by up-regulating the transcription factors of CBF and downstream genes in the cold stress pathway. With cold-sensitive bacterial strains, rice's *OsCSP1* and *OsCSP2* were examined for their ability to adapt to the cold. Both genes were found to be capable of compensating for the loss of bacterial CSP genes, indicating their significance in plants' ability to adapt to cold stress (Muthusamy et al. 2021).

6.4 Glycine-rich RNA-binding proteins (GR-RBP)

Glycine-rich RBPs (GRPs) are among those RBPs that have been extensively studied in plants, and the genomes of rice (*Oryza sativa*) and *Arabidopsis thaliana* each contain eight and six GRP genes, respectively. GRPs possess a C-terminal region that is rich in glycine and a conventional RRM at the N-terminus (Lee and Kang, 2016). It is a class IV GRP. The four subgroups IVa (RRM motif), IVc (CSD and two or more zinc-finger motifs), IVb (RRM and a CCHC zinc-finger motif), and IVd (two RRMs) of glycine-rich RBPs are distinguishable based on their domain features. Generally, GR-RBPs are functionally conserved across plant species (Muthusamy et al. 2021).

For instance, the rice genes *OsGRP1* and *OsGRP4* successfully rescued the cold-sensitive phenotypes of *atgrp7*, whereas *OsGRP6* was a different gene that gave the *atgrp7* plants freezing tolerance. By raising the amounts of indole-3-acetic acid in transgenic lines, *AtGRDP2* overexpression increased *Arabidopsis'* ability to withstand salt stress and enhanced growth. In contrast, over-expression of *AtGRP7* improved freezing tolerance while producing phenotypes in *Arabidopsis* that were vulnerable to salinity and drought. When exposed to cold stress, *AtRZ1a*serves as a RNA chaperone and helps *Arabidopsis* tolerate cold.

6.5 Serine/Arginine-Rich (SR) Domain

Serine/arginine-rich (SR) proteins function as RNA-binding proteins (RNA-BPs) and play significant roles in processing and regulating the splicing of precursor-mRNA (pre-mRNA). SR proteins contribute markedly to the process of alternative splicing by acting on the splice site. The highest quantity of SR proteins are found in flowering plants when compared to different eukaryotes, e.g., 24 in rice; 17 in *Brachypodium*; 18 in *Arabidopsis*; 12 in humans*,* and 7 in *C. elegans* (Iida and Go 2006; Longman et al. 2000; Manley and Krainer 2010; Barta et al. 2010; Vogel et al. 2010). Hence, SR proteins are considered the key regulators of the gene regulation mechanism (Duque 2011).

A broad analysis of SR gene expression in *Arabidopsis* was done by reverse transcriptase-polymerase chain reaction (RT-PCR). It did not show any changes in the overall transcript levels that are influenced by stress, but changes in temperature and salt condition repressed SCL33 (Palusa et al. 2007). However, under different abiotic stress circumstances, including high salinity, temperature, and UV irradiation, the alternative splicing pattern of various *Arabidopsis* SR protein family members exhibits significant changes (Lazar and Goodman 2000; Palusa et al. 2007; Tanabe et al. 2007; Filichkin et al. 2010). The splicing of downstream targets may be altered by stress-related environmental changes, like light, heat, and salt, in the SR protein gene products, leading to adaptive transcriptome modifications (Filichkin et al. 2010).

RBPs' functional roles are still being explored in the development and growth of plants concerning stress response mechanisms. The essential function of RBPs in organellar RNA metabolism under abiotic stress is being investigated. Genome-wide analysis of these RBPs will determine the fate of RNA during mutation and how these are engaged in the development and growth of plants.

Conclusion

Plants adopt a series of responses (stress resistance, avoidance, or defense) for responding to abiotic stress, an action carried out with the help of RBPs. Even though the functions of RBPs in plants are still being explored, there are some unanswered questions on the essential roles and capability of RBPs in plants' abiotic stress physiology. As an important component of plants' adaptive process in different environmental conditions, RBPs operates by regulating the splicing of pre-mRNA, RNA export, RNA stability, polyadenylation, and chromatin modification. With an outstanding understanding of RBPs in other life forms, RBPs' role in plants is still limited. Future research can be directed toward using these RNA-binding proteins as targets and understanding how RBPs recognize their substrates to regulate RNA metabolism to develop stress-resilient crops by focusing on the genomic and epigenomic mechanisms during abiotic stress conditions.

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