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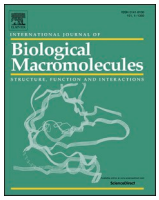

Review

From genes to traits: Trends in RNA-binding proteins and their role in plant trait development: A review

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ABSTRACT

RNA-binding proteins (RBPs) are essential for cellular functions by attaching to RNAs, creating dynamic ribonucleoprotein complexes (RNPs) essential for managing RNA throughout its life cycle. These proteins are critical to all post-transcriptional processes, impacting vital cellular functions during development and adaptation to environmental changes. Notably, in plants, RBPs are critical for adjusting to inconsistent environmental conditions, with recent studies revealing that plants possess, more prominent, and both novel and conserved RBP families compared to other eukaryotes. This comprehensive review delves into the varied RBPs covering their structural attributes, domain base function, and their interactions with RNA in metabolism, spotlighting their role in regulating post-transcription and splicing and their reaction to internal and external stimuli. It highlights the complex regulatory roles of RBPs, focusing on plant trait regulation and the unique functions they facilitate, establishing a foundation for appreciating RBPs' significance in plant growth and environmental response strategies.

1. Introduction

RBPs are critical components of cellular machinery and play crucial roles in regulating various plant traits and processes by modulating gene expression at transcription and post-transcriptional levels [1,2]. After transcription, mRNA molecules are bound by RBPs that can alter splicing, polyadenylation, and other modifications that determine the mRNA's maturity and functionality. Additionally, it plays a crucial role in mRNA stability and degradation, controlling the half-life of mRNA molecules within the cell and thereby regulating the levels of protein synthesis by cellular demands and environmental cues [3,4]. RBPs are characterized by their capability to bind RNA via specific RNA-binding domains (RBDs). RBPs are a broad group that can be split into two main types: conventional RBPs, which connect with RNA through one or more standard RBDs, and unconventional RBPs that do not have typical RBDs yet can bind to mRNA, as evidenced by methods like RNA interactome capture (RIC) [5,6]. These domains include the RNA recognition motif (RRM), K homology (KH) domain [7], zinc finger domain (C-×8-C-×5-C-×3-H type) [8], double-stranded RNA binding domain (DS-RBD) [9], cold shock domain (CSD) [10], and Pumilio/FBF (PUF) domain [11]. Additionally, RNA helicases contain highly conserved DEAD/DEAH boxes (Asp-Glu-Ala-Asp/His motif) [12]. The wide variety of RBDs is critical for recognizing specific RNA sequences and determining the functions of RBPs, which enables them to perform a broad range of cellular functions.

One of the most significant roles of RBPs in plants is regulating alternative splicing (AS), which enhances the flexibility of the plant transcriptome. This process is crucial for regulating the expression of specific genes and producing multiple transcripts, which in turn generate diverse proteins [13]. RBPs have been implicated in regulating splicing events during seed germination, root development, and flowering, as well as in the plant's response to biotic and abiotic stresses [14]. Plants, being immobile, rely on intricate control mechanisms within their transcriptomes to adapt to changing environmental

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conditions [15]. In plants, RBPs response to environmental changes and stress conditions. They respond to biotic and abiotic stresses such as drought, salt, and cold by regulating the stability and translation of mRNAs that encode proteins crucial for stress responses [16]. As versatile regulators, RBPs are vital to various biological processes in plants, including seed germination, root growth, stem cell maintenance, flowering, and seed development, through their influence on RNA metabolism [14,17–19]. Hence, RNA-binding proteins (RBPs) are vital for regulating gene expression in plants, primarily through alternative splicing, which enhances transcriptome flexibility and contributes to protein diversity essential for numerous biological processes.

Recent advancements in technology have facilitated the discovery of the RNA-binding proteome. UV crosslinking of RNA and RNA-interacting proteins, combined with oligo(dT) capture, is employed to uncover new RBPs [20–22]. RNA interactome capture (RIC) has revealed 1145 RBPs, including 595 previously unidentified candidates [23]. These techniques allow for the identification of numerous RNA-binding proteins (RBPs) and their interactions with RNA at a genome-wide scale, revealing a complex network of regulatory mechanisms [24]. Docking studies complement these findings by providing structural insights into specific interactions. Based on canonical RNA-binding domains (RBDs), bioinformatic predictions have identified over 800 RBPs in *Arabidopsis thaliana*, *Oryza sativa*, and *Zea mays* [25] Thus, the complex mix of different domains in RBPs leads to a wide range of structural and functional variability, allowing RBPs to modify and manage nearly all facets of target RNA metabolism and functionality.

To know about the significance of RNA-binding protein, we performed bibliographic mapping for the RNA-binding protein in plants. We used keywords such as RNA binding protein AND plants in the Scopus database as a result, we found 186 documents. These were further filtered by subject area, most relevant document type such as research articles, reviews, and book chapters, keywords and the language English as a result, we found 82 documents. Based on these documents, bibliographic mapping was performed. Each node represents a keyword, while different colors represent clusters and links represent the association between clusters. Greater the size of the circle indicated a greater contribution of the data to a specific field (Fig. 1). Likewise, we also evaluated the main contribution of different countries to the field (RNA-binding protein). Each circle represents a different country. The greater size of the circle revealed that these countries contributed mostly to the work on RNA binding proteins in plants such as the United States followed by Germany, the United Kingdom, Japan, and China (Fig. 2).

Overall, the RNA binding proteins are vital for the regulation of gene expression in plants, and bibliographic mapping can provide insights into their functional diversity and research trends. These proteins are integral to the complex regulation of gene expression in plants, impacting growth, development, and stress responses. Through bibliographic mapping, researchers can gain valuable insights into the trends, collaborations, and gaps in RBP research. This comprehensive understanding paves the way for innovative biotechnological applications that can enhance crop resilience and productivity, ultimately contributing to sustainable agricultural practices. As research in this field continues to evolve, it holds the promise of significant advancements in plant science and agriculture. This approach helps in identifying areas for future investigation and potential biotechnological applications.

Thus, this review aims to examine different domain characteristics of RBPs, covering their structural attributes and domain base functions. We will mainly focus on exploring the involvement of RBPs in plant trait regulation and their response to biotic and abiotic signals. We also highlight RBPs specific to the plant's post-transcriptional RNA processing mechanisms, including splicing, preserved across prokaryotic and various eukaryotic systems.

1.1. Brief overview of RBPs

RBPs are a large class of proteins that bind RNA and orchestrate the complex post-transcriptional gene expression regulatory network through their ability to influence the processing, localization, translation, and turnover of RNA molecules [26]. These proteins are ubiquitous and diverse, present in all life forms, and distinguished by having at least one RBD [5]. Through these binding domains, RBPs can bind to single-stranded or double-stranded RNA segments and interact with additional cellular elements via auxiliary domains [27]. They play pivotal roles in almost every aspect of post-transcriptional gene regulation, spanning events in both the nucleus and cytoplasm [28,29]. Through their interactions with mRNAs, RBPs assemble into dynamic, multi-part ribonucleoprotein complexes, representing mRNAs' active states [30]. The accurate assembly of these complexes is essential for precise regulation, ensuring the exact production of protein in eukaryotic cells [31].

RBDs are specialized regions within RBPs that directly interact with RNA molecules, determining these proteins' specificity, affinity, and regulatory roles [32]. RBPs exhibit diverse domain compositions and structural configurations, which enable targeted and effective functionality [33], and have the capability to bind to single or double-stranded (dsRNA), forming dynamic ribonucleoprotein (RNP) complexes [34]. The RRM is the most common RNA-binding domain, consisting of 80–90 amino acids that form a structure with a four-stranded beta-sheet aligned against two alpha-helices. It is known for its specificity towards RNA sequences and ability to interact with ssRNA. Proteins with RRM domains are crucial for multiple phases of RNA metabolism [35–37]. The hnRNP K-homology (KH) domain is one of the most prevalent RBD in both prokaryotic and eukaryotic proteins involved in gene expression regulation. This domain binds explicitly to nucleic acid sequences mediating responses to extracellular signals [38,39] PPR proteins are primarily located in mitochondria and chloroplasts, where they RNA metabolism processes [40]. PPR proteins consist of repeated motifs, about 35 amino acids long, in sequences ranging from 2 to 26 repeats, which primarily facilitate RNA-protein interactions despite their similarity to the tetratricopeptide repeat motifs known for protein-protein interactions [41]. The RGG box is a motif rich in arginine (R) and glycine (G) residues, often repeated in segments throughout the protein. This motif does not have a defined structure until it interacts with RNA, where it can then form various conformations to facilitate binding. RGG boxes are known for their role in RNA binding, modulation of RNA structure, and involvement in a range of RNA metabolic processes [42,43].

Another significant group of RNA-binding proteins includes the Asp-Glu-Ala-Asp-box (DEAD)-box helicases, known for their roles in RNA processing and export, RNP assembly, and translational control. These proteins feature seven distinct motifs within a segment of 350 to 400 amino acids [44,45]. Structural analysis of a typical DEAD-box helicase shows a dimeric arrangement, with each monomer comprising two structurally similar α/β domains in the polypeptide's N-terminal and C-terminal regions [46]. The double-stranded RNA-binding domains (dsRBDs) represent the second most prevalent family of RNA recognition motifs. These compact protein domains typically consist of 65–70 amino acids and feature an αββββα fold. They are essential in various post-transcriptional regulatory processes, such as RNA editing, miRNA biogenesis and function, and RNA export and localization [47,48]. GR-RBPs, recognized for their response to abiotic stress, are part of the fourth group within the, more prominent family of glycine-rich proteins (GRPs). These proteins feature a GRP segment at their C-terminal and an RRM at their N-terminal [49]. Within the, more prominent family of GRPs, there is a specific subgroup called RZs, which differ from other GRPs by having differs from other GRPs in that it has a CCHC-type zinc finger domain instead of an RRM. *Arabidopsis* genome has identified three distinct RZ genes: AtRZ-1a/1b/1c [50,51].

Analogous to prokaryotic cold shock proteins, plant cold shock

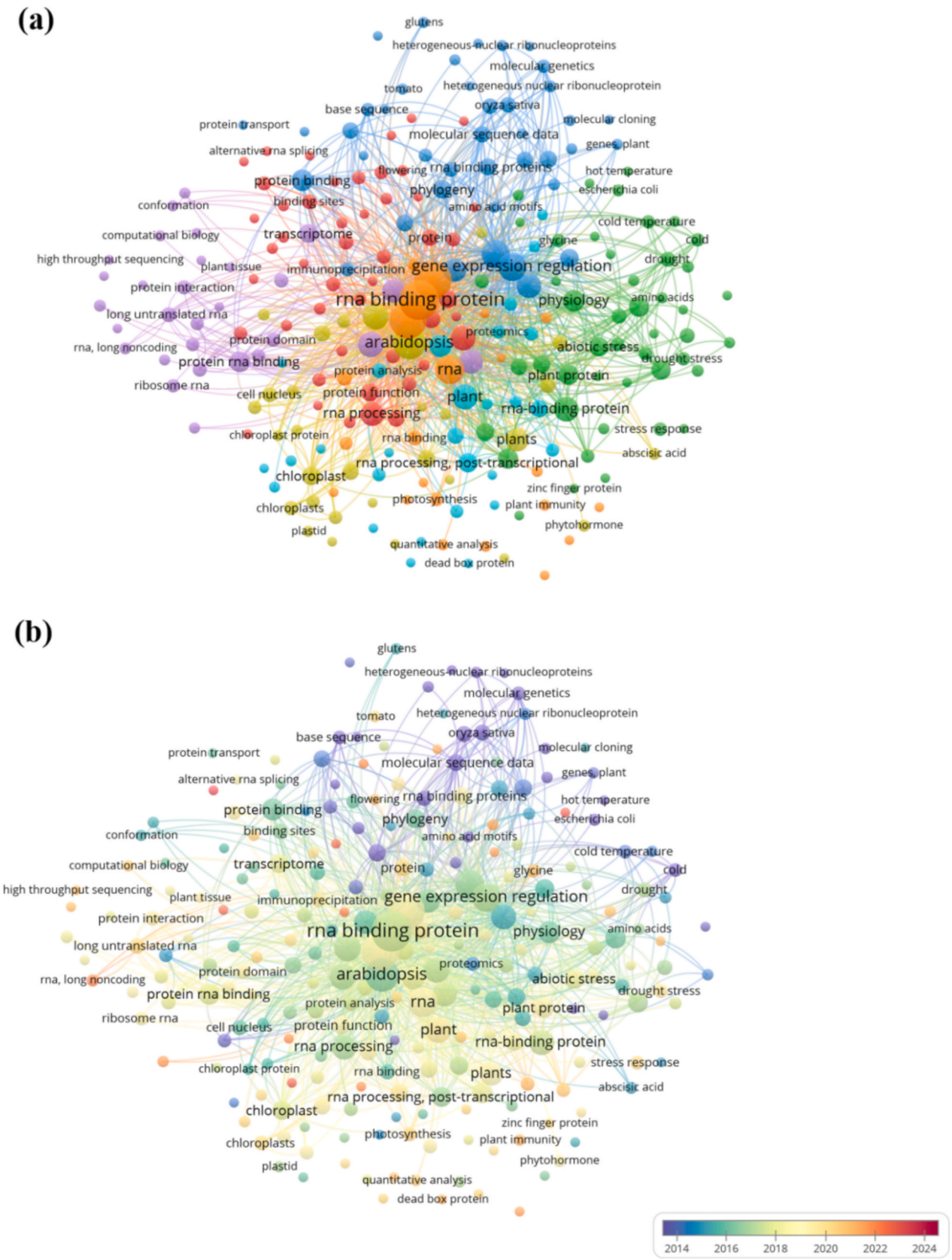

Fig. 1. A bibliometric network map of scientific research on the RNA-binging proteins in plants is gathered from data retrieved through Scopus. a) Different color clusters indicate the co-occurrence of the keywords RNA-binding proteins in plants and an overlay visualization. b) Specifies a period of the occurrence of the keyword from 2014 (blue) to 2024 (deep red).

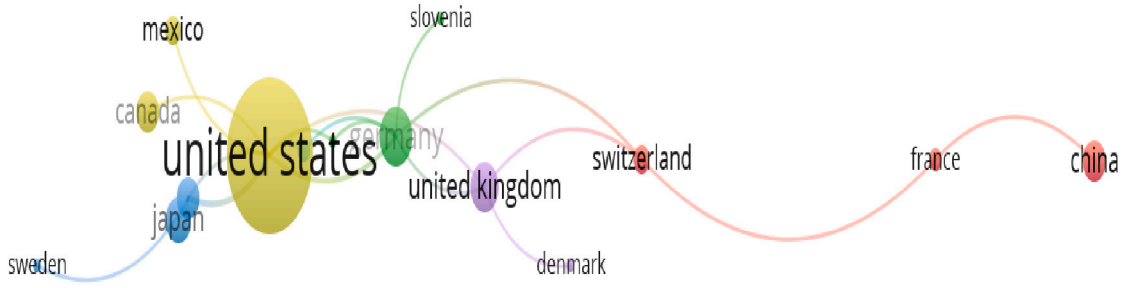

Fig. 2. Showing countries contributed mainly to the study of RNA-binding protein in plants.

domain proteins (CSDPs) feature a cold shock domain (CSD) that can bind both DNA and RNA, a function attributed to its well-preserved nucleic acid binding domain [52]. Specifically, in Arabidopsis, the mitochondrial *AtCFM9* plays a crucial role in splicing genes containing introns, essential for mitochondrial functionality [53]. Each RBD provides specificity to its corresponding RNA-binding protein (RBP) for a distinct set of RNA targets. In contrast, the precise RNA-binding preferences of RBPs remain a subject of ongoing research [54]. Recent advancements have unveiled a diverse array of RNA recognition motifs and other categories of RBPs, significantly transforming our understanding of RNA-protein interactions (Figs. 3–7) [55].

RNA-binding proteins are carefully localized throughout different cellular compartments to perform specific tasks, ultimately contributing to overall cellular functionality [56]. *AtGRDP2* is associated with RNA processing and translation proteins across distinct cellular locales: PABN3 in the nucleus, EF-1α in the cytoplasm, and CL15 in chloroplasts [57]. Despite significant progress in uncovering functional roles for various RBPs in living organisms in recent decades, our understanding of their specific plant functions remains significantly limited [58]. Numerous RBPs have distinct RBDs that selectively interact with RNA based on their sequence or structure. As vital gene expression regulators, RBPs contribute to fundamental cellular processes [59] (Fig. 3). RBPs often bind to short single-stranded RNA (ssRNA) sequences. However, specific RBPs interact with groups of RNAs that share common structural characteristics, including secondary and tertiary structural features, to support various biological processes [60]. Double-stranded RNAs (dsRNAs) play vital roles in diverse biological processes such as mRNA transport, RNA interference (RNAi), RNA editing, and the innate immune response [61]. Moreover, these proteins encompass auxiliary domains that fulfill diverse functions, such as facilitating protein-protein interactions or serving as targets for post-translational modifications. Common auxiliary domains in both plants and metazoans encompass glycine-rich and arginine-serine-rich domains (Fig. 8) [62,63]. Remarkably, the distinctive features of plant RBPs and their involvement in a range of stress responses point to a possible central role in plant-specific processes.

The PPR protein family is essential for regulating gene expression in organelles, particularly in RNA editing. These proteins utilize their modular repeat structure to bind RNA in a sequence-specific manner, guiding RNA modifications, stability, and translation. Each repeat typically binds one nucleotide of the RNA target, and the protein's interaction with RNA depends on the RNA sequence and specific motifs within the PPR protein. This docking indicates that the colored surfaces and labeled regions are involved in RNA recognition and binding. The PPR motifs align along the RNA strand, ensuring specific interactions with target sequences. The colored bonds represent an intricate network of hydrogen bonds, hydrophobic interactions, and other forces that stabilize the protein's structure and facilitate its interaction with RNA

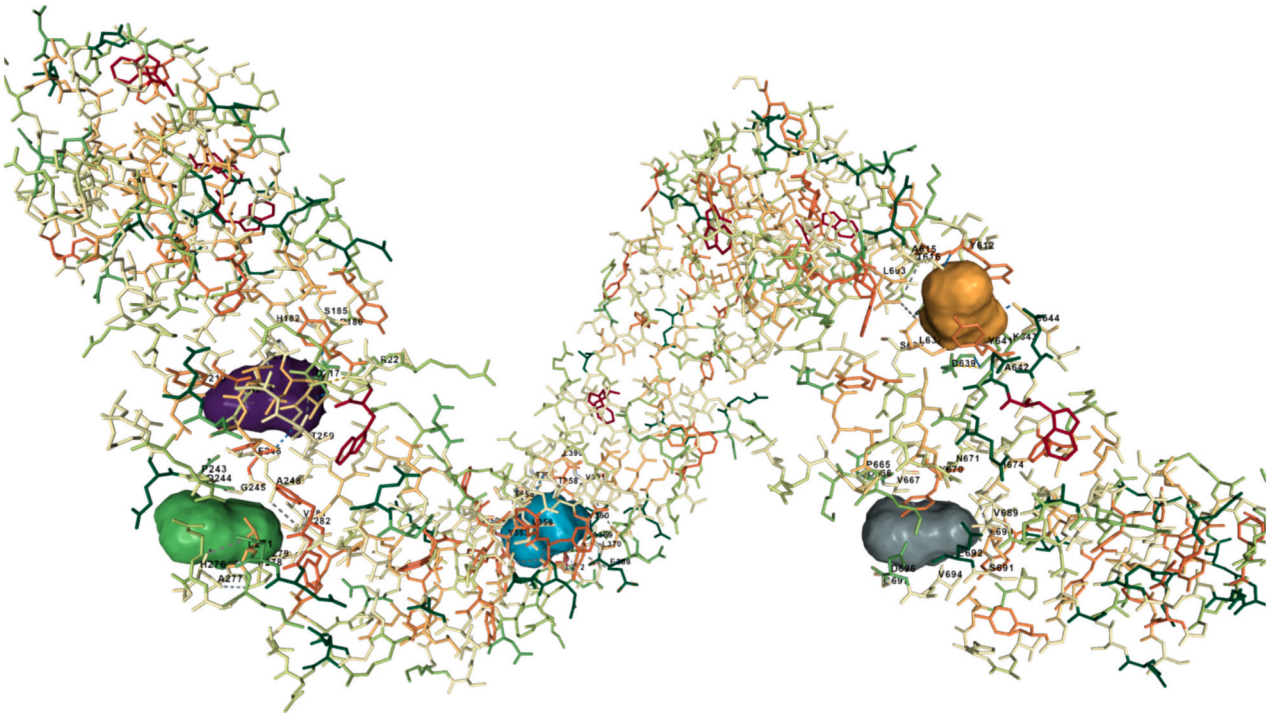

Fig. 3. Show a molecular structure of Pentatricopeptide Repeat (PPR) protein from *Zea mays*.

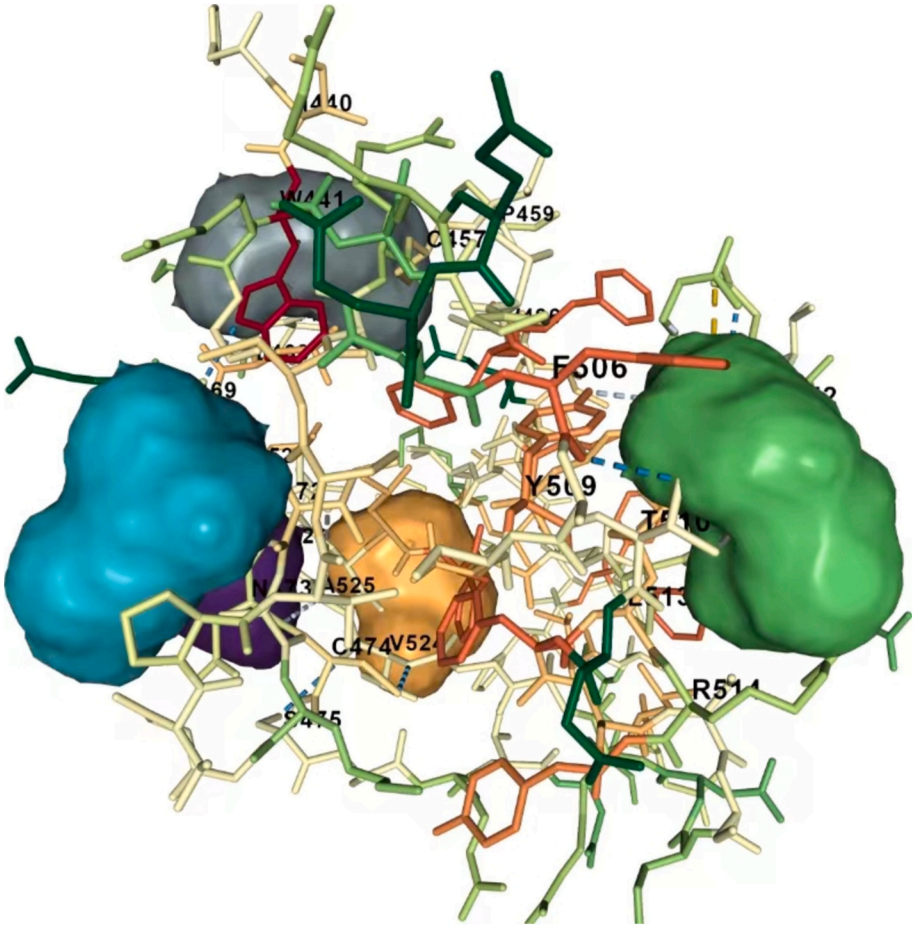

Fig. 4. The docking of a protein complex involving the SPOC domain of the Arabidopsis protein FPA. It's crucial for the regulation of flowering in *Arabidopsis* via FPA's role in processing the FLC antisense RNA.

(Fig. 3). Specific amino acids (e.g., S186, G246) are labeled to highlight key residues in the protein that may be critical for RNA recognition and binding. PPR proteins typically recognize specific RNA sequences through their motifs, and the labeled residues could be involved in these interactions. Some residues may contribute to the internal stability of the protein, ensuring proper folding and function. Certain residues might be directly involved in catalysis or modulating the protein's activity in RNA processing. Overall, this 4 m57 structure provides insight into how PPR proteins from *Z. mays* execute their regulatory functions by aligning with and modifying RNA in a highly specific manner.

The docking of a protein complex involving the SPOC domain of the *Arabidopsis* protein FPA is significant for regulating flowering time by controlling the alternative 3′-end processing of FLOWERING LOCUS C (FLC) antisense RNA. The FPA protein belongs to the split ends (SPEN) family. The SPOC domain is crucial for protein-protein and protein-RNA interactions necessary for transcriptional regulation (Fig. 4). It often acts as a scaffold for interactions with proteins involved in RNA processing, with colored regions representing potential docking sites. The labeled residues (e.g., F506, Y519) likely play important roles in RNA recognition, catalytic activity, or maintaining the protein's structure. These elements are essential for regulating flowering in Arabidopsis through FPA's role in processing FLC antisense RNA.

The molecular docking related to the YTH domain protein from *A. thaliana*, specifically the structure identified as "5ZUU" (Fig. 5), illustrates how this domain interacts with other molecules, such as ligands or potential binding partners. The interactions facilitated by YTH domain proteins like 5ZUU play a pivotal role in gene regulation, influencing mRNA processing and degradation pathways, and affecting gene expression levels in response to various developmental and environmental cues [64,65].

SAM domains mediate protein-protein or protein-RNA interactions and play a significant role in maintaining cellular structure and signaling. Fig. 6 shows the docking of the SAM domain and various interactions within the protein, focusing on different bonding types and regions. This structure indicates hydrogen bonding, essential for maintaining the tertiary structure of the SAM domain; these bonds can also bind with other molecules. The dashed lines help stabilize secondary and tertiary structures within the protein, ensuring the domain remains in the correct conformation for interacting with other proteins or RNA. The labeled residues, such as P194, K221, and R198, indicate key amino acids within the SAM domain that may be critical for protein interaction. Specific amino acids, particularly positively charged residues like arginine (R) and lysine (K), may interact with negatively charged residues or RNA molecules. Proline (P) and other hydrophobic residues could contribute to the protein's stability by forming hydrophobic cores within the domain. Some residues may serve critical roles in signaling or transcriptional regulation, depending on the function of the SAM domain in *Arabidopsis*.

The TPR motif is a structural element that mediates protein-protein interactions and is frequently observed in multi-protein complexes. Each repeat of the motif forms a pair of antiparallel alpha-helices, creating a binding groove for interaction with other proteins or molecules. The labeled amino acids (e.g., L227, R198, Q251) are critical residues within the TPR motif that may help stabilize the protein fold. Residues such as leucine (L227) and other hydrophobic residues contribute to the stability of the protein's alpha-helices by forming the

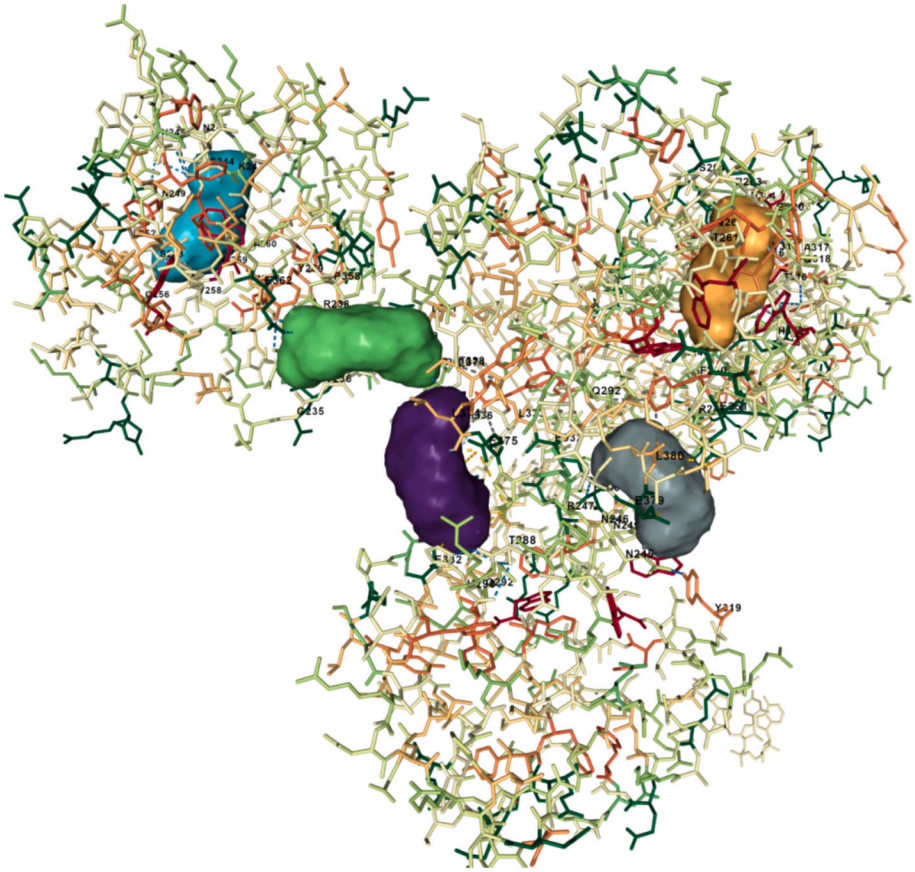

Fig. 5. The docking of YTH domain protein 5ZUU from *A. thaliana* not only elucidates its specific interactions but also enhances our overall understanding of RNA biology and protein interactions in plants. The interactions facilitated by YTH domain proteins like 5ZUU play a pivotal role in gene regulation.

protein's core. Charged residues, like arginine (R198) and glutamine (Q251), may facilitate binding to other proteins through electrostatic interactions, thereby enhancing the TPR motif's ability to mediate protein-protein interactions (Fig. 7).

All the aforementioned structures (PPR, SPOC, YTH, SAM, and TPR motifs) are involved in crucial interactions with either RNA or other proteins, mediating important cellular processes such as RNA editing, transcriptional regulation, and signaling. Each illustration uses colored surfaces to highlight functionally significant regions of the protein, showing binding sites and interaction domains.

1.2. RRM a leading domain in RNA binding

The RRM is a predominant domain in RBPs, known for its versatility in binding various RNA targets through diverse interaction modes involving beta-sheets, loops, and alpha-helices [37]. This variability allows RRMs to interact with multiple RNA sequences, showcasing their evolutionary adaptability to meet cellular demands [66]. Proteins with various RRM domains can simultaneously engage with several RNA molecules, utilizing a familiar protein-RNA interface and structural arrangement [67]. RRMs are extensively found in heterogeneous nuclear ribonucleoproteins (hnRNPs) and proteins that influence selective splicing. In eukaryotic proteins, RRMs often appear multiple times within a single protein (44 %) or are linked to other domains (21 %). They usually associate with zinc finger domains of the CCCH and CCHC types, the C-terminal domain of polyadenylate-binding proteins (PABP or PABC, 10 %), and the WW domain (9 %) [68]. In higher plants such as *Arabidopsis thaliana* and *Oryza sativa*, the variety of RRM proteins is considerable, highlighting their crucial role in RNA metabolism and plant trait regulation (Fig. 9) [68].

1.3. Collinearity analysis of the RRM gene family

The expansion and evolutionary conservation of the RRM gene family are evident through collinearity analysis. A comparative collinearity analysis between *O. sativa* and *A. thaliana* revealed that 20 pairs of RRM1 genes in these species were collinear [69]. This finding suggests that these 20 pairs of RRM1 genes may have conserved functions across both species and were preserved through evolution. Furthermore, the replication events of the RRM1 gene family in *Brassica rapa* were investigated to explore the underlying mechanisms driving the family's expansion. Intra-genomic collinearity analysis in *Brassica rapa* identified 89 collinear gene pairs linked to segmental duplication, indicating that this process significantly contributed to the expansion of the RRM1 gene family in *B. rapa* [70]. We have conducted the collinearity analysis of RRM gene family between rice and *Arabidopsis* by using TBtools software. In *O. sativa*, analysis of the replication patterns of the RRM gene family identified 68 gene pairs linked to segmental repetition. Inside the circle, ribbons represent the local alignments in four semi-transparent colors, blue, green, orange and red, representing the four quartiles up to the maximum score such as a local alignment with a score of 80 % of the maximum score is red, while one with 20 % of the maximum score is blue. Also, the bitscore correlates heavily with alignment, narrower and wider ribbons all describe alignments with 100 % identity.

This finding indicates that segmental duplication was a critical factor in the expansion of the RRM gene family in both *A. thaliana* and *O. sativa*. Comparative collinearity analysis between these species demonstrated that the RRM genes in *O. sativa* correspond directly with those in *A. thaliana*, indicating significant evolutionary conservation (Fig. 10). This conservation underscores the importance of RRM domains in maintaining essential RNA-binding functions across different plant species, thereby influencing plant growth and development through

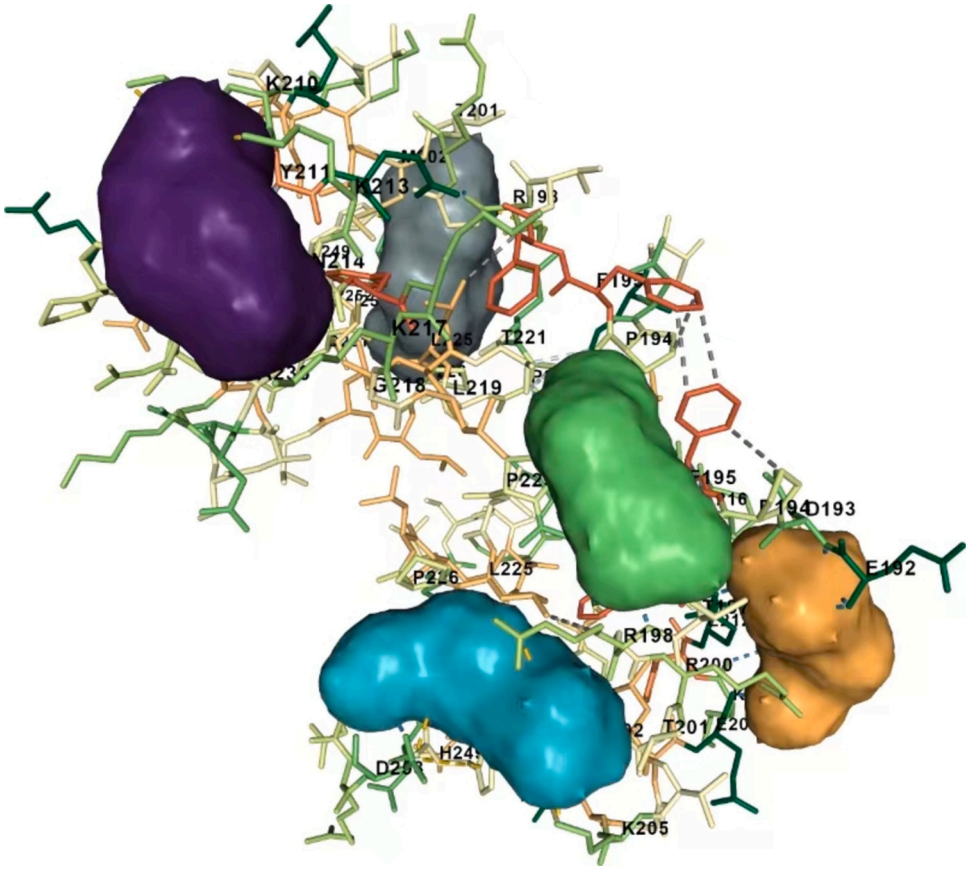

Fig. 6. The protein docking illustrates the structure of a SAM domain from *A. thaliana*. It typically mediates the assembly of protein complexes involved in signaling pathways, transcriptional regulation, or cytoskeletal organization in *A. thaliana*.

regulated gene expression.

2. RBPs play a crucial role in post-transcription regulation

RBPs regulate gene expression post-transcriptionally, influencing various stages of RNA's lifecycle, including synthesis, maturation, transport, and translation into proteins. RBPs closely interact with RNAs, governing their destiny through intricate regulatory mechanisms [71–73]. These proteins play critical roles in molecular functions such as splicing, 3′ end formation, RNA maturation, translation, and RNA degradation [65]. RBPs regulate gene expression post-transcriptionally alongside factors like microRNAs (miRNAs) and the spliceosome [74,75]. They form ribonucleoprotein (RNP) complexes that regulate RNA stability, alternative pre-mRNA splicing, mRNA decay, translocation, post-translational modifications, and RNA localization (Fig. 11) [76].

RBPs bind to RNA through RBDs, which are present in coding sequences, 5′ untranslated regions (5′UTRs), and 3′ untranslated regions (3′UTRs) [77]. These interactions influence RNA functions, including splicing, transcription efficiency, and stability. For example, interactions within the 3′UTR can promote or inhibit mRNA decay, impacting RNA stability [78]. Poly(A)-binding proteins (PABPs) are a critical subset of RBPs that regulate mRNA stability and translation. They bind to the poly (A) tail at the 3′ end of nearly all mRNAs, protecting them from exonucleolytic decay and interacting with factors at the mRNA 5′ cap to facilitate translation [79,80]. RBPs can affect the outcomes of pre-mRNAs and the RNAs they bind to, resulting in diverse outcomes such as alterations in splicing patterns, changes in stability, adjustments in translation levels, or shifts in localization [5,81]. Eukaryotic organisms must effectively control the expression of numerous genes to accomplish various biological functions crucial for growth and differentiation [82]. Ultimately, RNA-binding genes serve as central players in the intricate web of post-transcriptional regulation, shaping the expression of genes and influencing cellular function and organismal development.

2.1. RBPs involved in alternative splicing

RBPs regulate alternative splicing (AS), a process that increases the complexity of gene expression and is essential for plant growth and development [83]. AS allows a single gene to produce multiple mRNA variants, resulting in of various protein products essential for diverse cellular functions [84]. This variability is regulated by RNA-binding proteins (RBPs) and is necessary for generating diverse protein products [85,86]. In plants, up to 60 % of mRNAs undergo AS, contributing to protein diversity (Table 1) [87].

The fundamental process of intron removal is preserved across eukaryotes. It relies on complexes of proteins and RNA, such as small nuclear ribonucleoproteins (snRNPs), along with various RBPs that identify and excise introns [88]. Plant splicing is significantly influenced by the SR protein family, which is recognized for its RS domain and RRMs [89]. These proteins adjust spliceosome specificity, with the RRM binding to RNA sequences and the RS domain assembling other proteins necessary for splicing [90]. Nearly 90 % of genes encoding plant proteins contain introns, making intron excision during pre-mRNA splicing a crucial gene expression stage [91]. Alternative splicing is governed by diverse RBPs that detect cis-regulatory elements in pre-mRNAs and direct spliceosome activity [92]. The spliceosome, a large ribonucleoprotein complex, assembles at splice sites within pre-mRNA introns to facilitate intron removal through phosphodiester transfer reactions [93]. RBPs' regulatory function in splicing is shaped by their dynamic integration into messenger ribonucleoproteins (mRNPs) and interactions characterized by competition and cooperative recruitment

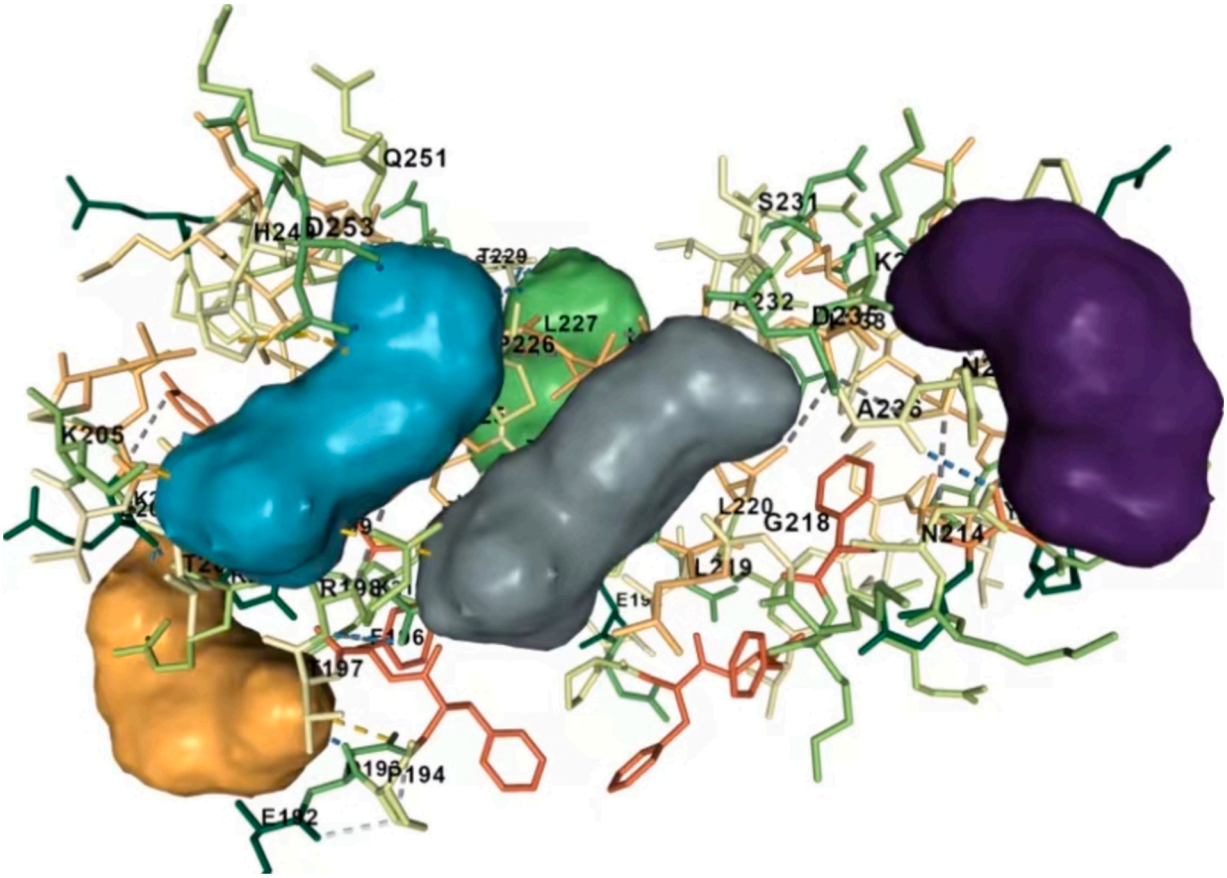

Fig. 7. The molecular structure of the Tetratricopeptide Repeat (TPR) motif of *A. thaliana*. The TPR motif is crucial for facilitating protein-protein interactions in various biological processes. The TPR motif's structure allows it to form a scaffold that binds to other proteins, contributing to protein folding, transport, and signaling pathways in *A. thaliana*.

[94]. The recognition of 5′ and 3′ splice sites, marking the beginning and end of each intron, involves U-rich snRNPs (U1, U2, U4, U5, U6) and non-snRNP splicing factors like *U2AF65*, U2AF35, and SR proteins [95,96]. U1 snRNP identifies the 5′ splice site through base-pairing, while the U2AF heterodimer attaches to the 3′ splice site [97,98]. Additionally, factors such as cis-acting elements, trans-acting factors, transcriptional activities, and chromatin organization manage the AS process [99,100]. SR proteins and hnRNPs are two major RBP families involved in splicing regulation [101,102]. SR proteins typically facilitate splicing [103], while hnRNPs often act as inhibitors [104]. These proteins are regulated at the expression level and post-translationally via signaling pathways, adjusting their function in specific tissues and cell types [105].

In plants, RBPs, such as Serine/Arginine-rich (SR) proteins, influence the splicing machinery's ability to recognize and process splice sites, thereby modulating AS [106]. such as SR proteins like *SR45* and *SC35* in *A. thaliana* are regulated by the SR protein-specific kinase II (SRPKII), which affects their phosphorylation status and subcellular localization, they are ultimately influencing the splicing and expression of genes like *FLOWERING LOCUS C (FLC)*, which controls flowering time [107]. RBPs also play significant roles in stress responses through AS [108]. The RALF1-FERONIA (FER) receptor complex regulates stress responses and growth by phosphorylating *GRP7*. This phosphorylation enhances *GRP7*'s mRNA binding capability and its interaction with the spliceosome component U1-70K, thereby facilitating splice site selection [109]. The *AtGRP7* modulates alternative splicing by binding to pre-mRNAs. In *Arabidopsis,* RZ-1B and RZ-1C roles are pivotal in controlling RNA splicing, promoting efficient splicing of the *FLOWERING LOCUS C* transcript, which encodes the floral repressor. However, these proteins also inhibit *FLC* transcription, consistent with the high *FLC* levels and delayed flowering observed in rz-1b rz-1c mutants [65,110] (Fig. 12). RBPs and their corresponding RNPs roles are pivotal in mRNA splicing within the plant transcriptome. For instance, *FCA* and *FPA*, two RBPs with RRM domains, regulate flowering time by reducing FLC mRNA levels through alternative polyadenylation [111]. Other polyadenylation factors, including FY, hnRNP A1-like protein 1 (HLP1), and *AtCPSF100*, impact FCA pre-mRNA polyadenylation, influencing flowering timing [57]. Overall, RNA-binding proteins are crucial for regulating alternative splicing, ensuring accurate gene expression, and appropriate responses to internal and external signals in plants.

2.2. RNA helicase

RNA helicases have a central domain composed of two RecA-like domains (RecA1 and RecA2) connected by a flexible linker. This domain includes up to 12 conserved motifs crucial for RNA binding, NTP attachment, and unwinding using ATP hydrolysis [131,132]. This unwinding is essential for spliceosome assembly and splicing catalysis [133]. RNA helicases are crucial in the spliceosome's process of identifying splice sites, which aids in excluding introns and assembling exons. Eight specific RNA helicases are fundamental for pre-mRNA splicing across all eukaryotic organisms [134]. These enzymes are classified within the Superfamily 2 (SF2) helicases, featuring two RecA-like domains and various extensions at their N- or C-terminals. While SF2 helicases typically function independently as monomers, some can form homo-dimers [135]. They possess common motifs that facilitate NTPs (commonly ATP) binding and hydrolysis and interactions with nucleic acids. For instance, Motif III is vital for mediating the

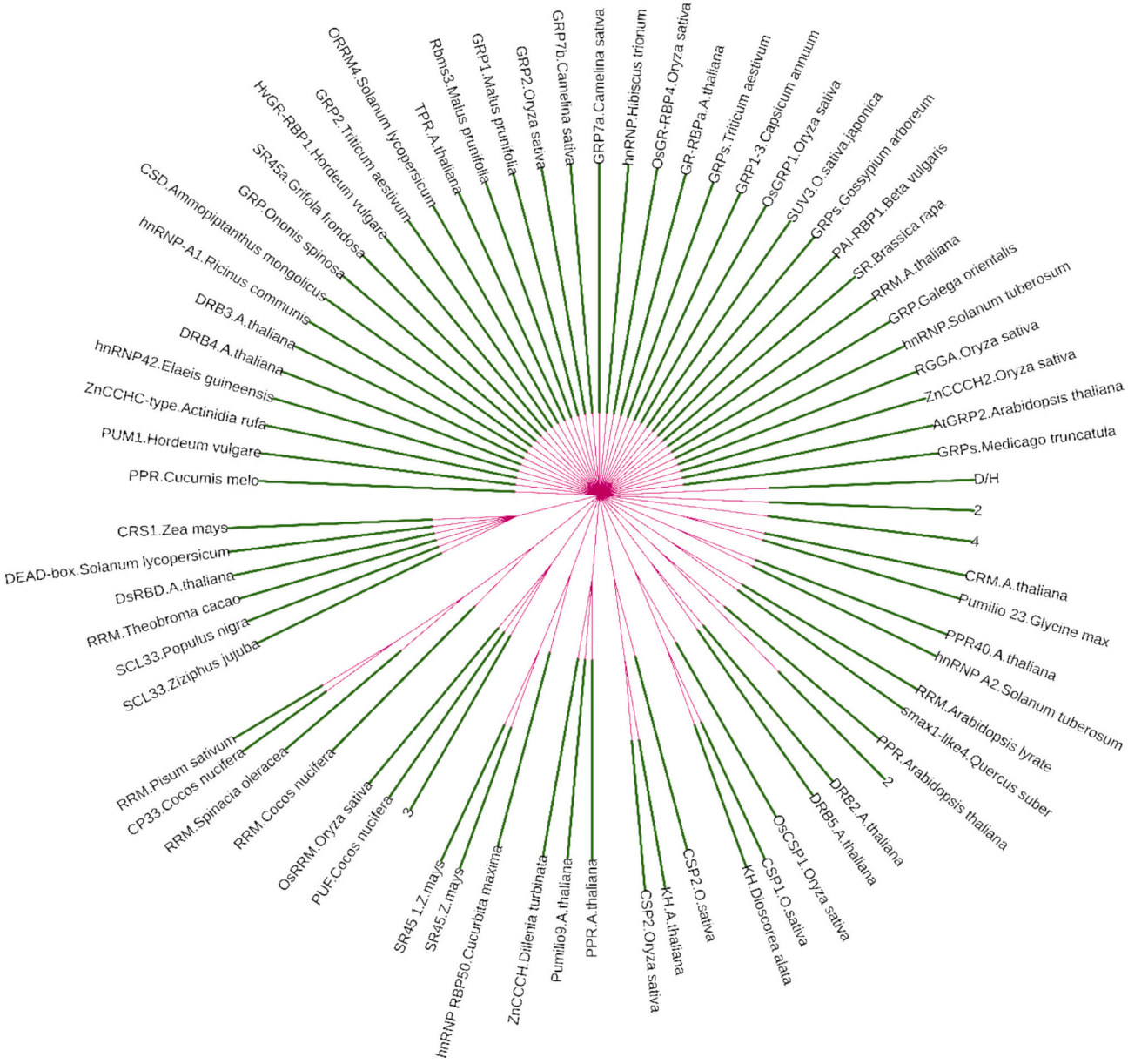

Fig. 8. The evolutionary relationships among taxa were assessed using the Neighbor-Joining method. The bootstrap consensus tree, derived from 1000 replicates, illustrates evolutionary history. Branches with less than 50 % bootstrap support were condensed. Evolutionary distances, measured in terms of amino acid differences per site, were computed using the p-distance method. This analysis utilized 74 amino acid sequences, with gaps and missing data excluded (complete deletion option), resulting in a final dataset of 3 positions. The evolutionary analyses were conducted using MEGA11.

interactions between nucleotide-binding and nucleic acid-binding motifs [136]. Variations in these motifs contribute to the differing activities across helicase families. Among the eight critical spliceosomal RNA helicases, three—Prp5, Sub2, and Prp28—are members of DEAD-box family [133], four—Prp2, Prp16, Prp22, and Prp43—belong to the DEAH-box, and one, Brr2, is categorized as a member of the Ski-2-like family [137]. DEAD-box helicase DDX3X unwinds RNA duplexes by engaging with a dsRNA, projecting a conserved alpha-helix within the RecA1 domain that disrupts the duplex structure, leading to strand separation and ATP hydrolysis [138]. DEAH-box RNA helicases unwind RNA duplexes by translocating along one strand and displacing the complementary strand. They shift from an open to a closed state during ATP hydrolysis, then revert to an open state to establish new contacts with the RNA [139]. In *Arabidopsis*, DEAD-box RNA helicases play a significant role in both vegetative and reproductive growth. They regulate alternative splicing events and rRNA processing, which are essential for the translation of genes that control growth under various environmental conditions. Additionally, DEAD-box RNA helicases are involved in liquid-liquid phase separation, which is crucial for the organization of cellular compartments and metabolic efficiency during stress responses [140]. Furthermore, DExD/H-box RNA helicases support plant growth by participating in ribosomal RNA biogenesis, a key process in the production of ribosomes required for protein synthesis [141]. These helicases ensure the proper folding and remodeling of ribonucleoprotein complexes, which are essential for cell growth, division, and responses to environmental changes such as drought and cold.

Both DEAD-box and DEAH-box RNA helicases have been found to play a role in plant stress responses. For instance, specific DEAD-box RNA helicases in tomatoes, such as *SlDEAD23* and *SlDEAD35*, have been linked to abiotic stress and virus infection responses. This implies that these helicases have a variety of functions in stress response mechanisms [142]. Hence, DEAD-box and DEAH-box RNA helicases are

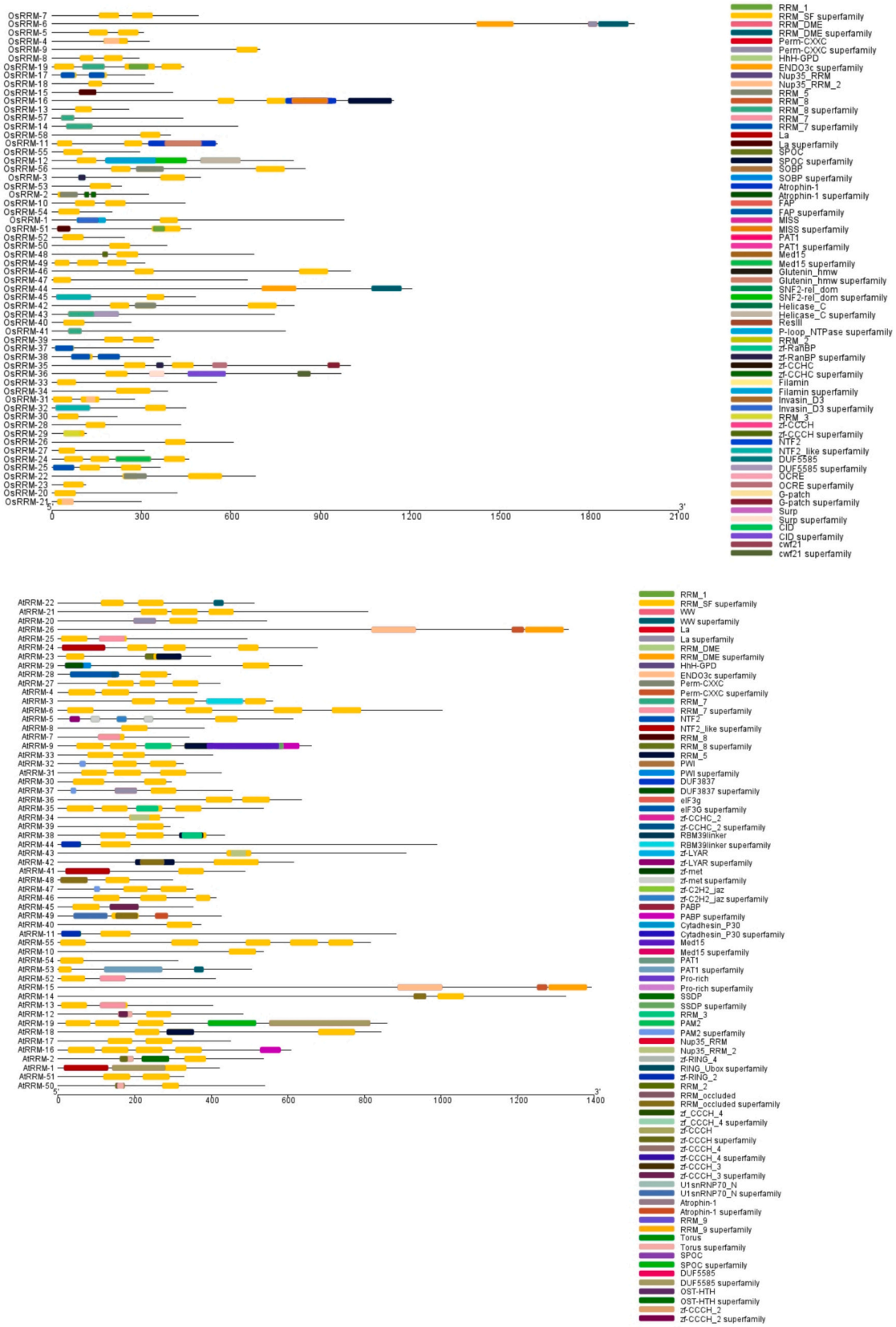

Fig. 9. The motif analysis of the RRM gene family in the *Oryza sativa* and *Arabidopsis thaliana* model plants. Motif analysis has distributed the 58 and 55 members of the RRM gene family in *O. sativa and A. thaliana* across 65 and 82 subfamilies, respectively. Each colored box represents a motif, and the gray line represents a non-conserved sequence.

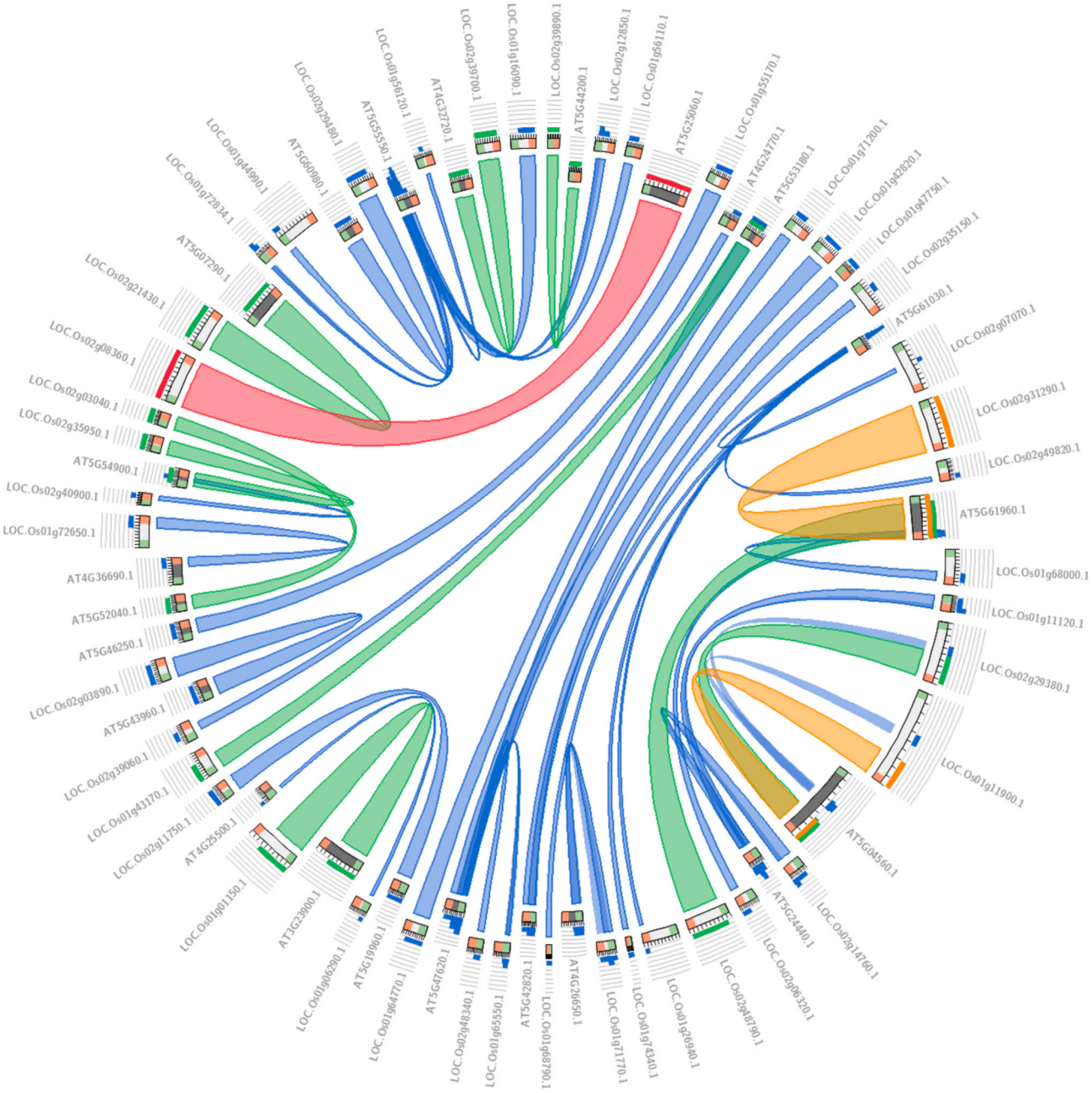

Fig. 10. Collinearity analysis of the RRM gene family shows blue, green, red, and orange lines representing the relationships between RRM gene family members in *Arabidopsis thaliana* and *Oryza sativa*. The outer layer's various colored modules denote different chromosomes, while the central layer displays a line graph and heat map indicating gene density across these chromosomes.

crucial for pre-mRNA splicing and stress responses, underscoring their critical role in cellular adaptability and function.

2.3. PUF proteins

The PUF is a large group characterized by a conserved RBD known as the Pumilio homology domain (PUM-HD), which is crucial for RNA interaction [143]. These eukaryote proteins feature a unique PUM-HD comprising eight aligned α-helical PUF repeats forming a crescent shape at the C-terminal [144]. The number of repeats varies human Puf-A and yeast Nop9 have eleven, while Arabidopsis *Pum23 (APUM23)* has ten [145,146]. Pumilio proteins bind to the 3′-untranslated regions (3' UTRs) of target mRNAs to regulate mRNA stability and translation, often working with other proteins [147]. In humans, Pumilio proteins *PUM1* and *PUM2* play a critical role in gene expression control by interacting with the CCR4-NOT deadenylase complex, which is essential for mRNA degradation and maintaining transcriptome integrity [148]. PUF proteins can either repress or activate target mRNAs, showcasing their complex regulatory roles. In plants, PUF proteins also act as post-transcriptional suppressors. For instance, *APUM5* is involved in responses to biotic and abiotic stresses. Overexpressing *APUM5* in plants increases salt and drought stress sensitivity at various growth stages by binding to the 3' UTR of stress-responsive genes [81,149]. In Arabidopsis, the Pumilio protein *APUM24* is crucial for the maturation of seeds, indicating the essential roles of PUF proteins that extend beyond RNA degradation and translational regulation. *APUM24* impacts the BPM-WRI1 regulatory pathway, influencing seed oil accumulation and size, for significantly enhancing crop yield [150]. Thus, the PUF family

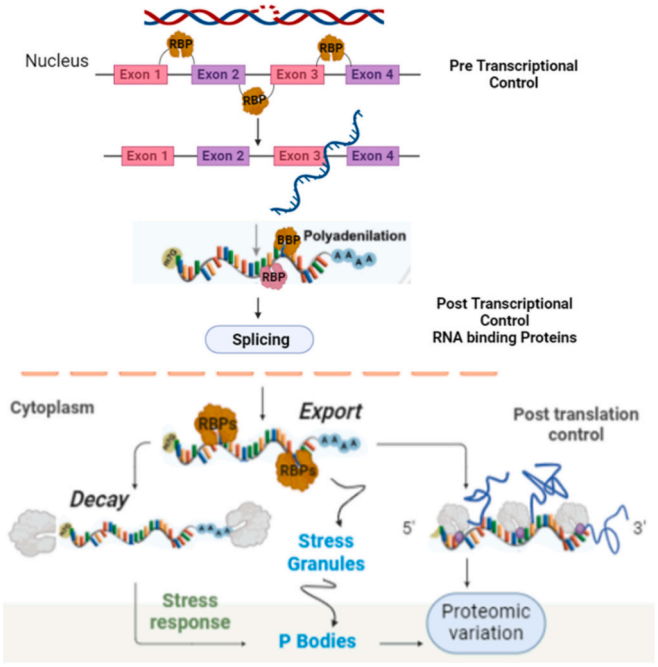

Fig. 11. RNA regulation is governed by RBPs from the nucleus to the cytoplasm, which select alternative exons during splicing and determine alternative polyadenylation sites. They regulate the splicing of multi-exon genes and the exon skipping results in different protein isoforms from one unique gene. The RNA nuclear export by RBPs determines the proper out in the amount and correct timing from the nucleus. Following RNA export, at the post-translational level, specific RBPs regulate mRNA function by engaging in mechanisms such as decoying or protection protecting against degradation. They respond to signals such as the formation of dynamic stress granules and P-bodies or ensure mRNA performance by facilitating translation within polysomes, thereby maintaining a high rate of peptide-protein expression. All these processes occur at the post-translational level.

of RBP is essential for gene regulation, stress responses, and developmental processes across various eukaryotic organisms.

2.4. Drosha and dicer

Drosha and Dicer are essential RNA-binding proteins that play pivotal roles in microRNAs (miRNAs) biogenesis, which are crucial for plant gene regulation [151]. Drosha initiates the miRNA processing pathway by cleaving primary miRNAs (pri-miRNAs) into precursor miRNAs (pre-miRNAs) within the nucleus. Dicer then processes these pre-miRNAs into mature miRNAs in the cytoplasm [152]. These mature miRNAs become part of RNA-induced silencing complexes (RISCs), guiding them to target mRNAs for either cleavage or translational repression [153].

Drosha and Dicer help fine-tune gene expression by regulating the levels of specific mRNAs, thereby influencing various physiological and developmental processes such as drought or high salinity; the miRNAs generated through the actions of Drosha and Dicer modulate the expression of stress-responsive genes, enhancing the plant's ability to survive and adapt [154]. Moreover, these proteins regulate genes that control plant growth and morphology, ensuring optimal development and functioning under varying environmental conditions [155]. Dicer's function is vital for gene regulation, development, and the cellular response to various stresses [156]. Conversely, Drosha and Dicer are foundational to the miRNA biogenesis pathway, intricately involved in regulating gene expression, and pivotal for cellular function and response mechanisms.

Table 1
RNA-binding proteins involved in splicing of RNAs.

Protein	Specie	Function	RBD	Reference
EIN2	*Oryza sativa*	Splicing	RRM	[112]
SR45	*A. thaliana*	Splicing	SR	[113]
SR45a	*Brassica rapa*	Splicing	SR	[114]
GRP1	*Z. mays*	Splicing	hnRNP-like glycine-rich	[115]
AtRZ-1c	*A. thaliana*	Splicing	GRP	[110]
NbRZ-1 A	*Nicotiana benthamiana*	mRNA alternative splicing	GRP	[116]
CFM4	*A. thaliana*	Splicing	CRM	[117]
CRS1 CRS2	*Z. mays*	Splicing	CRM	[118]
PGR3 PPR5 PPR10	*Z. mays*	splicing	PPR	[119]
WSL	O. *sativa*	Splicing	PPR	[120]
PGN	*A. thaliana*	Splicing	PPR	[121]
OsCFM2	*O. sativa*	splicing and ribosome maturation	CRM	[122]
NSRs	*Medicago truncatula*	Splicing	SR, RRM	[123]
SR45a	*Gossypium australe*	Splicing	SR	[124]
BvSATO1	*A. thaliana, Beta vulgaris*	Splicing	PAI-RBP1	[125]
AtSKRP	*A. thaliana*	Splicing	PRP, SR	[126]
FgRbp1	*T. aestivum*	Splicing	SnRBP (U2AF23)	[127]
OsGRP3 OsGRP162	*O. sativa*	Splicing	GRP, U1/U2 spliceosomal factors	[128]
SRRM1L	*A. thaliana*	Splicing	RRM, RS	[129]
GRP7 GRP8	*A. thaliana*	Splicing	GRP	[130]

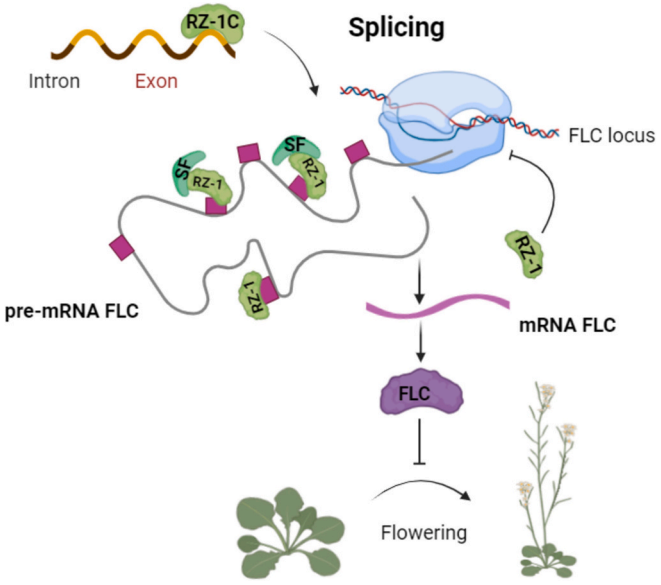

Fig. 12. RZ-1C promotes co-transcriptional splicing at the *FLC* gene. Initially, RZ-1C prevents *FLC* transcription. However, when RZ-1C binds to the *FLC* gene during transcription, it stimulates co-transcriptional splicing via interacting with proteins involved in splicing. As a result, full-length *FLC* mRNA is produced, which leads to the creation of a protein that inhibits flowering.

3. The regulation mechanism of RBPs

The regulation of RBPs is vital for cellular function as it influences RNA molecule fate and gene expression control [157]. These proteins interact with RNA directly and indirectly and are key players in RNA metabolism regulation. The abundance of RBPs in plant genomes suggests their significant roles in plant development, growth, and stress adaptation [54]. Specific RBPs, such as GRPs, RZ proteins containing zinc fingers, CSDPs, and RHs, are characterized by an RRM at the N-terminus and a GRP domain at the C-terminus. These RBPs play essential roles in plant development and responses to stress [158,159]. The importance of RBPs in intron splicing and their impact on plant growth and development are well-established. Proteins like U11/U12-31K and U11/U12-65K, members of the seven minor spliceosomal snRNPs involved in U12-type intron splicing, are critical for proper development in both dicot and monocot plants [159,160]. In *Arabidopsis*, the ABA-regulated ARP1, located in the nucleus and responsive to ABA, modulates the expression of several genes related to gene regulation. The overexpression and knockout of ARP1 have been linked to delayed germination under conditions of ABA exposure, salinity, and dehydration, emphasizing ARP1's role in post-transcriptional RNA regulation during seed germination [161]. RBPs are vital in plant physiology, impacting growth, development, and stress responses by intricately regulating RNA metabolism and gene expression.

3.1. Inner and outer signals that regulate RBPs

In plants, RBPs are regulated by various internal and external signals that influence their role in gene expression and development [162]. RBPs like *AtGRP7* are influenced by circadian rhythms, which integrate temporal signals to modulate their activity, ensuring proper timing for various physiological processes [55]. The regulation of RBPs in plants involves a complex interplay of internal molecular mechanisms and external environmental signals, emphasizing their vital role in maintaining plant growth, development, and stress responses. RBPs are prevalent in plants and essential for controlling gene expression by managing RNA metabolism in response to internal and external stimuli. They are essential elements among the numerous factors that affect considered essential elements among the multiple factors affecting gene regulation in plant eukaryotes (Table 2) [163,164].

Post-transcriptional modifications, involving changes in transcript abundance, stability, and protein synthesis, are essential mechanisms that allow plants to quickly adjust their transcriptome and proteome in response to hormonal signals and environmental challenges [165,166]. This integration of signals at the RNA level allows cells to respond to internal and external stimuli, thereby playing a vital role in their environmental adaptation [167]. Plants also coordinate flowering time by integrating internal and external signals [168,169]. Alternative splicing (AS) adjusts gene expression in response to environmental factors like light and temperature, with higher temperatures prompting earlier flowering in *A. thaliana* [170]. RBPs, such as GR-RBPs and CSDs, facilitate plants to adapt to cold, salinity, and drought conditions [55]. Abiotic stress, such as high salinity and temperature fluctuations, induces changes in RNA-binding protein activity, often mediated by plant hormones like abscisic acid (ABA). For example, ABA stimulates the phosphorylation of the RNA-binding protein AKIP1 in fava beans, enhancing its binding to target mRNAs [171,172]. Plants rely on RBPs to regulate gene expression in response to various biotic and abiotic challenges. RBPs play crucial roles in post-transcriptional defense mechanisms against pathogens by interacting with RNA, thus activating disease-resistance transcripts that ensure plant immunity [166]. Plants utilize extracellular vesicles (EVs) to transport small RNAs (sRNAs) to fungal pathogens, thereby suppressing genes associated with virulence through cross-kingdom RNA interference (RNAi). RNA-binding protein Argonaute 1 (AGO1) and RNA helicases such as RH11 and RH37 play roles in loading small RNAs into extracellular vesicles, which are vital for plant immunity against pathogens like *Botrytis cinerea* [173]. The regulation of RBPs in plants involves a complex interaction of internal molecular mechanisms and external environmental signals. This dynamic regulation is essential for maintaining plant growth, development, and stress responses, underscoring the pivotal role of RBPs in plant biology.

3.2. Genetic variation of RNA binding gene and trait regulation

Variability in plant traits includes differences in how they grow when they flower, their ability to withstand environmental pressures, and their overall output. This variability can be affected by the diversity of RNA-binding genes, which regulate the expression of genes critical for defining these traits (Table 3) [207,208].

3.2.1. Influence of RNA-binding proteins on flowering time regulation

The requirement for vernalization in wheat, enabling it to flower sooner, is tied to its genetic complexity due to being polyploid. In wheat breeding, significant attention is given to the heading stage, as highlighted by Hyles et al. [209]. Genes involved in the vernalization process, including Vrn1, responsible for a MADS-box transcription factor play a crucial role [210]. Vrn1 can, under specific conditions and after prolonged cold exposure, initiate the activation of Vrn-B3, thereby hastening the shift to reproductive stages, as explained by Benaouda et al. [211]. Notably, the absence of Vrn1 does not prevent wheat from flowering and seed production, indicating it is not vital for these processes [212]. This reveals that additional genes linked to flowering are involved in the ability of wheat varieties to adapt to diverse climate conditions. Vernalization triggers a regulatory cycle involving Vrn1, Vrn2, and Vrn3, with support from *TaGRP2*, VER2, TaVRT2, and TaFDL2, initiating the onset of wheat's heading and flowering, as noted by Liu et al. [213]. The study of Blackmann et al. [214], also explored *AtRGGs*' functions in rgg mutants, uncovering an early flowering trait affected by different growth temperatures, indicating *AtRGGs*' interaction with specific mRNAs for floral initiation. In *epi* transcriptomic modification, N6-methyladenosine (m6A) plays a crucial role in regulating flowering time through transcript stability [215]. The m6A demethylase ALKBH10B eliminates m6A modifications from mRNAs by recognizing and targeting specific m6A sites. Reduced ALKBH10B activity delays flowering, whereas its overexpression accelerates it. ALKBH10B directly interacts with *FT* and *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 3/7* (*SPL3/7*) mRNAs, leading to demethylation and influencing flowering time in mutants with altered function [55,216]. Thus, the dynamic role of RBPs in RNA processing and stability plays a crucial role in regulating development and responding to environmental changes. Additionally, *ORRM4* (*GR-RBP5*) and *ORRM5* (*GR-RBP2*) are essential for proper plant development. Mutants with loss-of-function in *A. thaliana* show reduced growth and delayed flowering, attributed to defects in mitochondrial RNA editing [217].

RBPs play a crucial role in regulating flowering time by precisely integrating diverse signals through various pathways [218]. *AtGRP7,* regulated by the circadian clock, is known for its involvement in splicing regulation and affects the timing of flowering by interacting with the MADS-box inhibitor FLC. Without *AtGRP7*, FLC levels increase, resulting in delayed flowering in the atgrp7–1 mutant. Conversely, high levels of *AtGRP7* promote the development of the inhibitory FLM-β variant [219] Similarly, *AtGRP20* regulates RNA splicing, and flower development is conserved among some angiosperms [220]. Thus, GRPs impact MADS-Box transcription factors through multiple pathways in of regulating flowering timing.

Another protein, HRLP (hnRNP R-LIKE PROTEIN), inhibits the cotranscriptional splicing of the FLC gene, a key repressor of flowering. This action leads to the formation of R-loops near the first intron of the FLC gene, suppressing its activity and promoting flowering in *A. thaliana*. HRLP, along with the *ARGININE/SERINE-RICH 45* splicing factor, forms nuclear condensates with fluid characteristics essential for

Table 2
The different RBPs and their role in various biotic and abiotic signals.

RBPs (Domain)	Genes	Genes response internal & external stimuli	Species	References
K-homology domain	*esr1–1* *esr1–2*	The heat resistance	*Arabidopsis thaliana*	[174]
CSDP	*OsCSP1* *OsCSP2*	respond and adjust to cold stress.	*Oryza sativa*	[175]
PAZ, Piwi, RdRP	*JcDCL1, JcAGO1, JcAGO4, JcRDR5, JcRDR6a*	play key roles in responding to various stresses, including cold, drought, salt, deficient nutrient solution, and BA.	*Jatropha curcas*	[176]
Zinc-finger-containing RBPs	*BrRZ1*, *BrRZ2*, *BrRZ3*	response to salt and drought stress.	*B. rapa*	[177]
YTH	*CitYTH1*	Receptive to signals triggered by cold temperatures.	*Citrus sinensis*	[178]
	ECT1	SA-dependent stress response	*A. thaliana*	[179]
	CsYTH1, CsYTH2, CsYTH4	exhibit increased expression levels in response to cold stress	*Cucumis sativus*	[180]
	GhYTH8	Response to Drought Stress	*Gossypium species*	[181]
SR	*BrSR1,2,4, BrRS2Z2–5, BrRSZ1, BrRSZ3, BrSCL4,5, BrSR-like 2*	exhibit elevated expression levels in response to cold stress.	*Brassica rapa*	[182]
	Sl-RS28, *Sl-RS29*, *Sl-RS42*, *Sl-RS46a*	heat stress	*Solanum lycopersicum*	[84]
	MeSR34	improved salt tolerance.	*Manihot esculenta*	[106]
	CPR5	Regulation of plant immunity.	*A. thaliana*	[183]
	SR45a	immune responses	*Gossypium australe*	[124]
GR-RBP	*(CsGR-RBP)3*	exhibited notable upregulation in cucumber fruit under low temperatures.	*Cucumis sativus*	[184]
	AtGRP7	significant in the resistance to Ni and Pb.	*Arabidopsis thaliana*	[185]
	ZmGRP2	Resist against infection	*Zea mays*	[186]
	NtGRP-1α *NtGRP-3*	Response to wounding continued to rise until peaking four hours into the stress period.	*Nicotiana tabacum*	[317]
	BoiRBGA13	response to NaCl-induced and cold stress conditions.	*Brassica oleracea*	[187]
	BpmiR396c governs the activation of *BpGRF3* through the targeting of *BpGRP1*.	key to salt tolerance	*Betula platyphylla*	[188]
	OsGRP3/OsGRP162	thermotolerance	*O. sativa*	[128]
	NbRBP3a	to suppress plant immunity	*Nicotiana benthamiana*	[189]
	OsGRP1 OsGRP4 *OsGRP6* *GR-RBP*	resistance to freezing.	*O. sativa*	[190]
	Ah.GR-RBP.1, Ah.GR-RBP.12, Ah.GR-RBP.3, Ah.GR-RBP.15	enhance resistance against infection	*Arachis hypogaea*	[191]
RGG-PAI-1	*RGGA*	response to drought signal	*Solanum tuberosum*	[192]
RRM	*RRM1*	response to cold stress, low temperature, and salt stress	*Brassica rapa*	[70][193]
	RBGD2/4	heat stress response	A. *Arabidopsis*	
	RBM25	stress response and regulation of gene expression	*A. thaliana*	[194]
	OsDEG10	Anoxia, salinity, cold, ABA	*O. sativa*	[195]
RRM-GR	*MpGR-RBP1*	response to drought	*Malus prunifolia*	[161]
RRM-CCHC-GR	*OsGRP1, OsGRP2, OsGRP4, OsGRP5, OsGRP6*	response to cold	*O. sativa*	[50]
PUF	*APUM9*	upregulated in heat stress	*A. thaliana*	[196]
SDP	*At1g12800*	heat stress	*A. thaliana*	[197]
Ribonucleoprotein (hnRNP)	*EgRBP42*	response to signals associated with salinity, drought, flooding, cold, and heat stresses	*Elaeis guineensis*	[198]
DEAD-RH	*SlDEAD31*	upregulated in heat stress	*Solanum lycopersicum*	[199]
	RH6/8/12	Plant Immunity	*A. thaliana*	[200]
	TCD33	cold stress	*O. sativa*	[201]
RGG box	*AtRGGA*	influencing tolerance to signals of salt and drought stress.	*A. thaliana*	[202]
Puf proteins	*APUM5*	defense-responsive gene that acts against infection by cucumber mosaic virus (CMV).	*A. thaliana*	[149]
Double-stranded RNA Binding (DRB) proteins	*DRB3* *DRB4* *DRB5*	defense genes that respond to signals from pathogens.	*A. thaliana*	[203]
DRPs	*GM6*	response to low-temperature stress	*Z. mays*	[204]
C2H2 zinc finger family protein	*ZAT17*	*acts as an inhibitory factor for Cd tolerance*	*A. thaliana*	[205]
PPR protein	*SOAR1*	modulating salt tolerance	*O. sativa*	[206]

Table 3
RNA-binding proteins and plant traits regulation.

RBPs (Domain)	Genes	Plant development	Species	References
RRM	*FCA*	flowering time	*A. thaliana*	[266]
RRM	*HRLP*	flowering time	*A. thaliana*	[221]
RRM	*Lgg*	regulates spikelet hull length	*O. sativa*	[267]
RRM	*RRC1*	flowering time	*A. thaliana*	[268]
RRM	*SFPS*	flowering	*A. thaliana*	[269]
RRM	*SlORRM4 ORRM5*	Delayed tomato fruit ripening	*S. lycopersicum*	[226]
RRM	*SC35 SCLs*	flowering time	*A. thaliana*	[270]
RRM	*SR45*	flowering time	*A. thaliana*	[221]
RRM	*SSF*	flowering time	*A. thaliana*	[271]
RRM	*UBA2C*	flowering time	*A. thaliana*	[272]
RRM	*GRP7*	Root development exhibited	*A. thaliana*	[273]
RRM	*OsRRMh*	flowering-late flowering and a larger panicle phenotype	*O. sativa*	[274]
GR-RRM	*ORRM4 GR-RBP5*	Slow development and delayed flowering	*A. thaliana*	[275]
ZN-GRBPs	*AtRZ-1b AtRZ-1c*	seed germination, leaf growth, and floral time	*A. thaliana*	[110]
ZN-GRBPs ZN-GRBPs	*TaRZ-2 TaRZ-3*	Overexpressing retards seed germination	*T. aestivum*	[276]
ZnF	*KHZ1 KHZ2*	flowering time	*A. thaliana*	[277]
ZnF	*SE*	leaf development	*A. thaliana*	[278]
zinc-finger RNA-binding proteins (RZs)	*BrRZ1 BrRZ2 BrRZ3*	seed germination and seedling growth	*B. rapa*	[279]
GPRs	*AtGRP2 AtGRP4*	flower and seed development, Overexpressing seeds delayed germination	*A. thaliana*	[49,62]
GPRs	*OsGRP1 OsGRP4 OsGRP6*	enhance seed germination	*O. sativa*	[280]
GPRs	*OsDOR1*	regulate seed dormancy	*O. sativa*	[281]
GPRs	*BnGRP1*	accelerates seed germination	*B. napus*	[282]
GPRs	*HvGRRBP1*	involved in the timing of anthesis, senescence, and grain protein levels	*H. vulgare*	[283]
GPRs	*AtGRP7*	influence flowering time and improve grain yield	*O. sativa*	[237]
GRP	*VviGRPs*	involve in the seed development	*V. vinifera*	[238]
GRP	*TaGRP2*	Regulate flowering	*T. aestivum*	[284]
GRP	*ItGRP9*	Regulate flowering	*I. trifida*	[285]
GRP	*SlRBP1*	regulation of fruit size and Fruit ripening	*S. lycopersicum*	[225]
GRP	*RZ1 A-Like (RZ1 AL)*	tomato ripening, particularly in fruit coloration	*S. lycopersicum*	[286]
GRP	*LeRBP1*	fruits maturation at green stage	*S. lycopersicum*	[287]
GRP	*VviRZ-1A VviGRP2 VviGRP3 VviGRP5 VviGRP7*	mesocarp development	*V. vinifera*	[238]
GRP	*CsGR-RBP3*	Fruit germination	*C. sativus*	[184]
GRP	*BnGRP1*	Accelerate seed germination	*B. napus*	[282]
GRP	*MpGR-RBP1*	Accelerate seed germination and seedling growth	*M. prunifolia*	[161]
Cold shock domain protein	*AtCSP4*	influences the late stages of embryo development	*A. thaliana*	[288]
DEAD-box RNA helicases	*RH SWA3*	embryogenesis or embryo development	*A. thaliana*	[289]
DEAD-box RNA helicases	*OsRH2 and OsRH34*	pollen and seed development	*O. sativa*	[290]
DEAD-box RNA helicases	*PLT1*	Regulate primary root growth and root meristem activity	*A. thaliana*	[291]
hnRNP	*HLP1 AtCPSF100*	regulating flowering time	*A. thaliana*	[292]
hnRNP	*StPTB StNova1*	Phloem translocation	*S. tuberosum*	[293]
hnRNP	*AtPTB1 AtPTB2*	seed germination	*A. thaliana*	[294]
hnRNP	*LIF2*	Cell identity during floral development	*A. thaliana*	[295]
LAM	*AtLa1-mediated gene*	Regulate Stem cell homeostasis	*A. thaliana*	[256]
RNA-binding protein (NSR)	*MtNSR1*	Root development	*M. truncatula*	[250]
CRM	*mCSF1 CFM9*	seed development and seedling growth	*A. thaliana*	[296]
PUF	*APUM9 APUM10 APUM11*	control of seed germination and dormancy	*A. thaliana*	[297]
PPR-	*GRP23*	embryo and kernel development	*A. thaliana*	[298]
PPR-	*PPR8522 EMP4), EMP5, CPSF30L*	Seed Development	*Z. mays*	[299,300]
YTH	*ECT2*	flowering time leaf development	*A. thaliana*	[301] [302]
SR	*SR 45*	regulating flower petal development	*A. thaliana*	[303]
SR	*LlSR28*	Pollen germination	*L. longiflorum*	[304]
SH3 domain-binding protein (G3BP)	*G3BP6*	Flowering regulation	*O. sativa*	[244]

controlling FLC splicing, R-loop generation, and recruiting RNA Polymerase II [221] (Fig. 13). These findings demonstrate that HRLP is crucial for preventing FLC splicing through these condensates, essential for reducing *FLC* levels and facilitating *Arabidopsis* reproductive success.

3.2.2. Impact of RNA-binding proteins on fruit ripening and development

The process of fruit ripening is complex and involves numerous changes in texture, color, flavor, and nutritional content. RBPs 'roles are essential in regulating these changes [222]. *MhYTP1* and *MhYTP2* expression increases during natural leaf senescence in *Malus pumila*. Overexpression of these genes in *A. thaliana* and *M. pumila* causes faster leaf yellowing and much lower chlorophyll levels than wild-type plants. *MhYTP2* can enhance maturity by interacting with acireductone dioxygenase 4, a protein associated with ethylene (ET) production [223]. Furthermore, fruits from *MhYTP1* and *MhYTP2* transgenic tomato plants

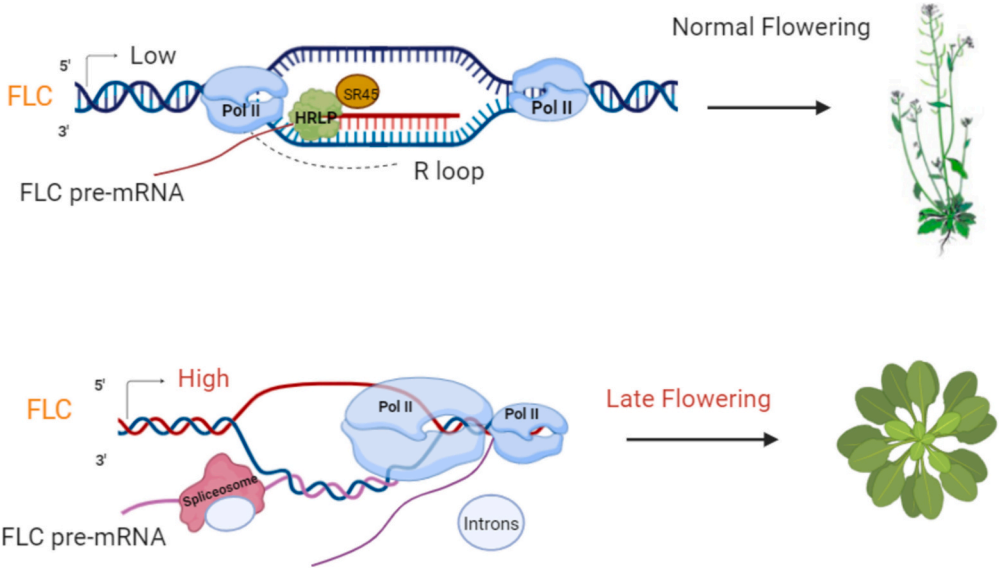

Fig. 13. HRLP regulates *FLC* cotranscriptional splicing by engaging in phase separation, which creates nuclear bodies close to the intron I of the nascent *FLC* RNA. These nuclear bodies serve multiple functions, such as inhibiting splicing, promoting the formation of R-loops, and impeding the recruitment of RNA Polymerase II near intron I. As a result, transcription of *FLC* is suppressed. Without HRLP the failure to establish nuclear bodies, the cotranscriptional splicing of *FLC* introns becomes easier. This reduces the formation of R-loops and facilitates the recruitment of RNA Polymerase II near intron I. Consequently, *FLC* mRNA levels increase, leading to a late-flowering phenotype.

became yellow earlier than fruits from wild-type plants, demonstrating that these YTH domain-containing genes can speed up tomato fruit ripening [224]. Ten *CitYTH* genes were discovered in *C. sinensis*, and their expression profiles were studied across diverse tissues and phases of fruit development [178].

RBPs are essential in the early stages of fruit development as they influence cell division, expansion, and differentiation. SlRBP1 has been found in tomatoes as an RBP that regulates the translation of its target RNAs to keep chloroplasts functioning properly. SlRBP1 deletion causes dwarf growth and yellowing leaves, whereas silencing the SlRBP1 miRNA produces much smaller fruits [225]. Furthermore, knocking down tomato *SlORRM4* causes delays in fruit ripening and abnormalities in mitochondrial RNA editing due to significant changes in the editing of target RNAs [226] (Fig. 14). Overall, RBPs are essential for fruit development and ripening, influencing processes such as cell division, expansion, differentiation, and the regulation of critical metabolic pathways. These processes ultimately affect the fruit's texture, color, flavor, and nutritional content.

3.2.3. Genetic regulation of pollen and seed development

PPR proteins have been associated with genetic variations that influence traits such as pollen development and seed setting [227]. In maize, the *ZmLARP6c1* gene encodes a pollen-specific protein that likely participates in RNA regulation within pollen. Expression analysis reveals the critical role of *ZmLARP6c1* in pollen tube growth, which is essential for fertilization in maize [228]. Pentatricopeptide repeat (PPR) proteins play a vital role in mitochondrial RNA processing during seed development. In maize, the PPR78 protein is essential for stabilizing nad5 mRNA, which is critical for the assembly of mitochondrial complex I. When the PPR78 function is lost, this process is disrupted, leading to developmental issues in seeds, including defective embryogenesis and abnormal endosperm formation [229]. Therefore, RNA-binding proteins

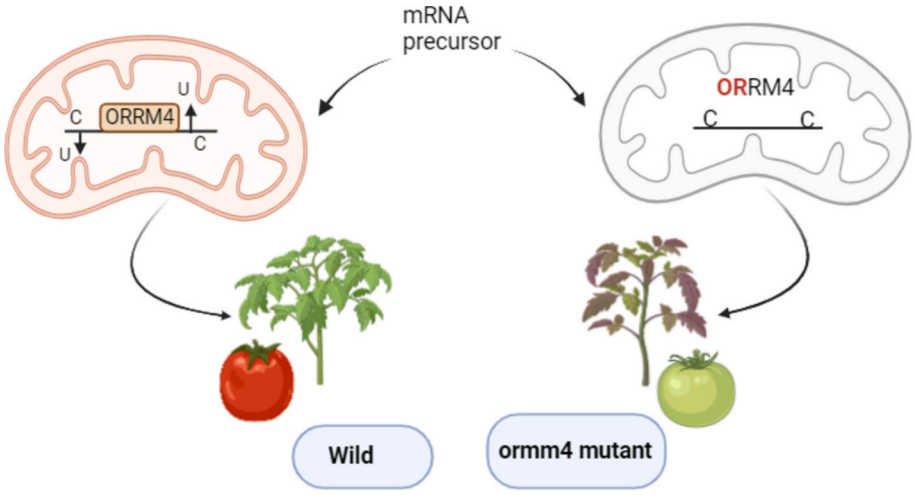

Fig. 14. Impact of *SlORRM4* on fruit ripening in tomatoes. This illustrates the wild-type tomato plant showing regular expression of *SlORRM4* in the mitochondria. This enables proper mitochondrial RNA editing and normal ripening, ultimately leading to the production of red tomatoes. In contrast, the orrm4 mutant, characterized by the knockout of *SlORRM4*, disrupts mitochondrial RNA editing, resulting in delayed fruit ripening.

(RBPs) are key to ensuring energy production during seed development. Moreover, RBPs are also involved in alternative splicing during this stage. For example, the RNA-binding protein DEK42 in maize is necessary for the alternative splicing of pre-mRNA during kernel development. Mutations in the dek42 gene result in abnormal kernel formation, highlighting the importance of splicing regulation for proper seed development [230].

RNA polymerase II *C-terminal domain phosphatase-like protein 1* (*CPL1*) is a DsRBD-type RNA-binding protein typically involved in seed germination behavior [231]. Recent research has indicated that CPL1 and CPL2 also influence seed dormancy. The regulation of the DELAY OF GERMINATION1 (DOG1) transcript, a key quantitative trait locus specifically controlling seed dormancy in Arabidopsis, is tightly controlled at multiple levels [232,233]. *APUMILIO PROTEIN24* (*APUM24*), an atypical Pumilio-homology domain-containing protein, plays a crucial role in regulating seed maturation by acting as a positive regulator that fine-tunes the BPM-WRI1 module. APUM24 decreases the mRNA stability of certain genes that promote degradation of WRI1, thus ensuring higher oil content and proper seed development. Therefore, *APUM24* is a promising target for breeding strategies aimed at increasing crop yields (Fig. 15) [150]. In maize, 18 *ZmPum* genes exhibited high transcriptional activity in the endosperm, particularly in seeds, highlighting the significance of the *ZmPum* family in early endosperm development [234]. Consequently, genes involved in RNA binding have a substantial influence on the diversity of traits in crops, enhancing both their quality and productivity. Glycine-rich proteins, which belong to the category of plant cell wall proteins, play a crucial role in this regard. The relationship between grain size and weight is critical for rice yields, as supported by Chen et al. [235]. By utilizing the MutMap technique, they demonstrated that rice mutant DGW1 encodes an hnRNP-like RNA-binding protein that contains two RRM domains. DGW1 interacts with *OsUBP1a* and OsUBP1b to form complexes that bind to GW6 mRNA, which plays a crucial role in regulating grain size. The absence of DGW1 produced results similar to those of GW6 deficiency, affecting grain size and hormonal responses. However, boosting GW6 expression in DGW1-deficient plants rectified the issue of grain size, as reported by Li et al. [236]. Consequently, this sheds light on the role of DGW1 in regulating rice grain size and weight through GW6 mRNA. Research on plant GR-RBPs has primarily focused on their impact on key agricultural traits [237]. Nineteen *VviGRPs* were identified in the grape genome, with seventeen expressed in ovules in stenospermocarpic grape varieties [238]. These findings indicate that GR-RBPs could offer valuable insights for seedless grape selection and breeding efforts. Additionally, the loss of function in *AtRZ-1b* and *AtRZ-1c* in Arabidopsis resulted in defective phenotypes, including delayed seed germination, reduced stature, and serrated leaves [110]. GRPs found in *Acer platanoides* are implicated in directly regulating the acquisition of seed dormancy [239]. Through extensive cloning and genomic analyses, researchers have identified the RBP-A-J-K complex, consisting of *RBP-K* (LOC_Os08g23120), RBP-A (LOC_Os11g41890), and RBP-J (LOC_Os10g33230), which has been shown to impact rice yield negatively. RBP-K enhances the activity of RBP-A and RBP-J, which influences growth regulators and subsequently impacts grain size and shape. RBP-A downregulates genes involved in growth pathways, affecting grain development and weight [240]. This evidence emphasizes the critical role of RBPs in post-transcriptional regulation, contributing to the variation of complex traits.

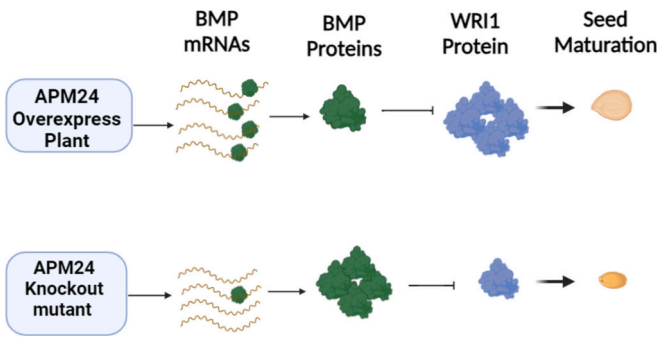

Fig. 15. A proposed model of APUM24 regulates seed maturation by tuning BPMs-WRI1.

3.2.4. Role of RNA-binding proteins in shoot and leaf development

The regulation of shoot development involves RNA-binding proteins (RBPs) that control the expression of genes responsible for shoot apical meristem function [55]. The Pumilio/FBF (PUF) family plays a vital role in maintaining stem cell populations within the shoot apical meristem by controlling mRNA stability and translation [241]. These proteins are crucial for properly forming and maintaining shoot tissues as they regulate the post-transcriptional control of key developmental genes [242]. Additionally, *AtPUM23* has been identified as an influencer of leaf morphology by modulating the expression of *KANADI (KAN)* genes. These *KAN* genes belong to the GARP family and play a significant role in establishing the abaxial identity of leaves [243]. G3BP is a member of the highly conserved RNA-binding protein group. Wang et al. [244] found that *G3BP6* levels increase during shoot maturation. RNA-sequencing and qRT-PCR tests demonstrated a decrease in miR156 levels in Col-0 during the development of shoots, whereas increased levels of pri-miR156a were observed in the g3bp6 mutant across all phases. Based on these findings, it can be inferred that *G3BP6* likely represses the level of miR156 by modulating miR156a transcription, which in turn regulates downstream targets such as SPL proteins during the blooming transition. Additional phenotypic assessments further confirmed that g3bp6 mutants with a loss of function displayed delayed flowering traits.

3.2.5. Role of RNA binding protein in senescence

RBPs play a crucial role in regulating plant senescence, the final phase of development characterized by cellular breakdown and nutrient recycling. During senescence, RBPs influence gene expression by managing the stability, splicing, and degradation of messenger RNAs (mRNAs) associated with senescence-associated genes (SAGs) [55]. These SAGs manage the degradation of cellular components, particularly in leaves, to redirect resources to developing seeds or young tissues.

A study on *Malus domestica* focused on YTH domain-containing RBPs, specifically MhYTP1 and MhYTP2. These RBPs promote leaf senescence and fruit ripening. Overexpressing these proteins accelerated senescence, suggesting their potential as marker genes for plant aging and their role in enhancing fruit quality by modulating ripening and senescence timing [224]. RBPs help maintain cellular homeostasis during senescence by selectively stabilizing or degrading specific mRNAs. For instance, under stress conditions such as nutrient deprivation, RBPs can stabilize mRNAs that encode proteins involved in nutrient recycling and the stress response, thereby delaying the onset of senescence. Conversely, RBPs can also target certain mRNAs for degradation to facilitate the orderly progression of senescence by ensuring the timely breakdown of cellular components [245]. The degradation of mRNAs by RBPs is especially important in promoting leaf senescence, where cellular resources are redirected from aging tissues to younger tissues or developing seeds [246]. RBPs (RNA-binding proteins) manage mRNA stability during senescence. They selectively stabilize mRNAs encoding proteins crucial for stress responses and nutrient recycling while targeting others for degradation to facilitate cellular breakdown [247]. This regulation ensures timely and efficient senescence, optimizing nutrient redistribution from senescing tissues to areas of active growth and storage. Additionally, RBPs regulate alternative splicing during senescence, contributing to transcript variants that fine-tune cellular responses to aging-related signals [248].

Hormonal pathways, particularly those involving ethylene and abscisic acid (ABA), are regulated by RBPs during senescence.

Interfering peptides that target protein-protein interactions within the ethylene signaling pathway delay plant senescence by inhibiting typical ethylene responses. These peptides interact with ethylene regulators and could serve as tools for managing senescence in agriculture [249]. So, RNA-binding proteins are central to regulating gene expression during plant senescence. They manage mRNA stability and degradation, interact with stress-responsive and hormonal pathways, and link environmental factors to aging processes. Thus, RBPs are central to the regulatory network that controls plant senescence, facilitating the transition from growth to aging.

3.2.6. *RNA-binding proteins in root*

Another well-characterized RBP is the nuclear speckle RNA-binding protein (NSR), which contains a C-terminal RRM domain. NSR has been extensively studied in *A. thaliana* and is known to modulate the alternative splicing of specific pre-mRNAs, including long non-coding RNAs (lncRNAs) like ALTERNATIVE SPLICING COMPETITOR (ASCO) [250]. NSRs interact with ASCO to regulate the alternative splicing of mRNAs involved in root development. By binding to ASCO, NSRs affect the splicing patterns of target mRNAs, leading to the production of protein variants essential for root formation [123], Furthermore, *GRP8* has been demonstrated to play a role in determining root hair cell fate under phosphate starvation conditions. This occurs through its interaction with *WRKY75*, thereby enhancing WRKY75 abundance. *WRKY75* directly regulates gene expression in phosphate (Pi) acquisition. Under Pi deficiency, *WRKY75* is upregulated and binds to the promoters of Pi transporter genes, thereby enhancing their expression. This upregulation enhances the plant's ability to absorb Pi from the soil, which is essential for sustaining growth and development in nutrient-limited conditions (Fig. 16) [251,316].

In root development, ALY RBP interacts with *UAP56*, linking mRNA export to the functions of root and leaf cells. This interaction features the essential role of RBPs in maintaining dynamic RNA transport and localization processes crucial for root growth [252,253]. *Arabidopsis* proteins RZ-1 A, RZ-1B, and RZ-1C feature a zinc finger motif positioned between the RRM domain and the C terminus. RZ-1B and RZ-1C function redundantly in regulating seed germination and other developmental processes under normal growth conditions. Mutants lacking both RZ-1B and RZ-1C exhibit significantly delayed germination rates and display abnormalities in roots and leaves compared to wild-type plants. This correlates with observed high expression levels of RZ-1C in embryos, germinated seed endosperm, and newly formed leaf and root tips demonstrating the vital function of RBPs in shaping root and leaf development through precise control of alternative splicing and gene expression [110]. Unveiling these molecular interactions opens exciting possibilities for enhancing crop resilience and productivity in diverse environments.

3.2.7. *Genetic control of embryo development by RNA-binding proteins*

Dek42 is a nuclear-localized protein consistently present in various maize tissues, encoding an RBP that influences alternative pre-mRNA splicing and maize kernel development. According to Zuo et al., [230], mutations in dek42 significantly modify the splicing patterns of active genes, particularly affecting U12-type introns. This mutation leads to a substantial reduction in DEK42 protein levels, which in turn disrupts the expression of numerous genes critical for kernel development. Despite its critical role in splicing regulation, DEK42's mutation significantly impairs normal gene expression and splicing mechanisms, thus causing developmental challenges in maize kernels.

LARPs consist of two RBDs called the La-module, which includes the LaM and the RRM [254]. The structural basis for the recognition of 3′-end poly(A) RNA by LARP1, a protein involved in La nuclear functions, has been clarified [255]. In plants, the *AtLa1* gene is essential for tRNA maturation and completion of embryogenesis in *Arabidopsis* [256]. In *Arabidopsis*, *AtLARP6c* is involved in post-transcriptional regulation of mRNA during pollen tube navigation towards the embryo sac in the ovule [257]. Similarly, in maize, *ZmLARP6c1* plays a critical role in the male haploid gametophyte during pollen tube germination, directing growth towards the embryo sac to facilitate sperm cell delivery for double fertilization [258,259]. These studies emphasize the vital roles of RBP in both plant development and reproduction, demonstrating their diverse roles, from regulating splicing to guiding pollen tubes for successful fertilization.

3.2.8. *RNA-binding proteins and vascular bundle development*

The vascular system of higher plants, comprising the xylem and phloem, serves as the primary transport network crucial for growth and development [260]. A novel translational regulatory mechanism involving the zinc-finger protein JULGI (JUL) and its targets, the 5′ untranslated regions (UTRs) of SUPPRESSOR OF MAX2 1-LIKE4/5 (SMXL4/5) mRNAs, has been identified specifically for phloem development. This regulatory module is conserved exclusively in vascular plants. JUL directly interacts with and induces an RNA G-quadruplex formation in the 5′ UTR of SMXL4/5, which is pivotal in promoting

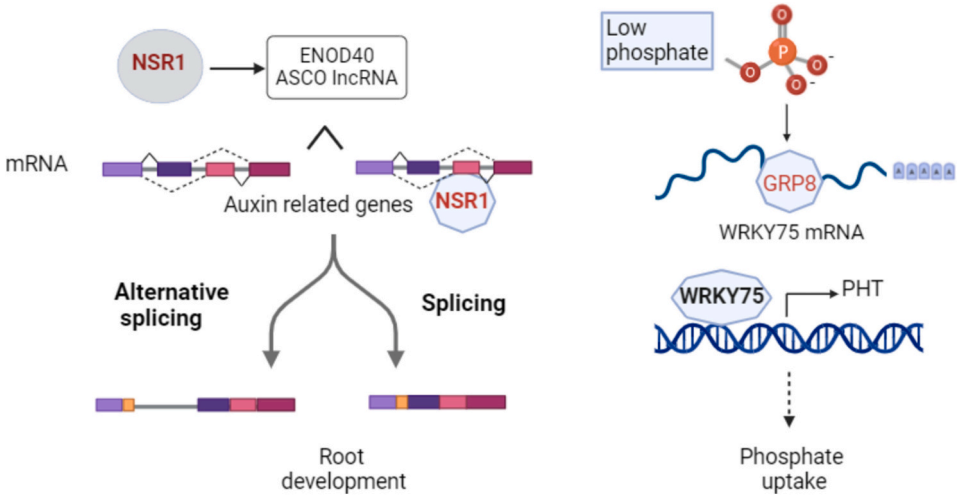

Fig. 16. NSR1 influences the auxin response in root development through its regulation of alternative splicing in auxin-related genes. It interacts with long non-coding RNAs (lncRNAs) ENOD40 and ASCO to modulate the splicing of crucial genes involved in root formation. In parallel, *GRP8* stabilizes *WRKY75* mRNA in low phosphate conditions, thereby enhancing the expression of phosphate transporter genes and improving phosphate uptake [216]. These interactions emphasize the crucial role of RBPs in gene expression and root development.

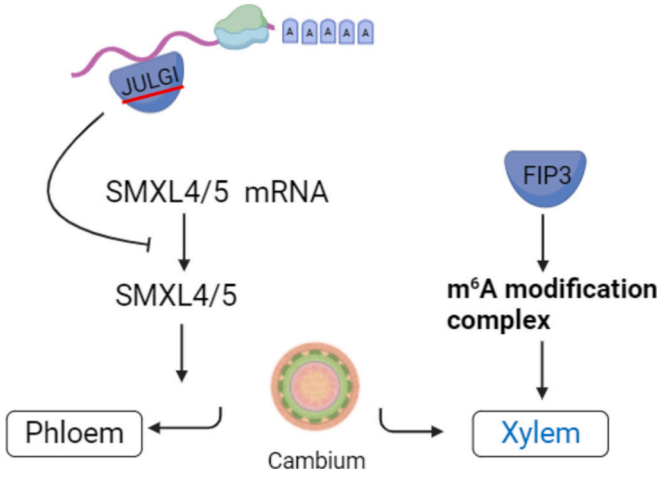

Fig. 17. RNA-binding proteins play a crucial role in vascular development. The zinc-finger protein JULGI (JUL) binds to the 5′ UTR of SMXL4/5 mRNA, forming an RNA G-quadruplex that inhibits translation and regulates phloem differentiation. FIP3, a component of the m6A modification complex, is essential for establishing xylem patterns.

phloem differentiation. The presence of the RNA G-quadruplex suppresses the translation of SMXL4/5, thereby regulating phloem differentiation (Fig. 17) [261].

In angiosperms, mRNAs involved in organ development are transported as long-distance signaling molecules via the phloem. This transportation is facilitated by ribonucleoprotein complexes formed by RBPs [262]. One essential RBP for the formation of such complexes is *CmRBP50*, a polypyrimidine tract-binding protein. *CmRBP50* undergoes phosphorylation at phosphoserine residues located at its C terminus, which allows it to directly interact with three proteins, forming a complex that binds mRNAs containing polypyrimidine tract-binding motifs, aiding their transport through the phloem sieve tube system [263]. RBPs in the phloem are essential for forming ribonucleoprotein complexes that transport RNA molecules over long distances, supporting the systemic delivery of RNAs to sink tissues and regulating developmental processes and responses to environmental stimuli [264]. In *A. thaliana*, Phloem Protein 16–1 (*AtPP16–1*) is involved in the systemic transport of RNA, crucial for coordinating growth between distant organs. *AtPP16–1* interacts with nucleic acids to facilitate their transport through the phloem, emphasizing the importance of RBPs in phloem function and plant development [265]. These dynamic interactions feature the essential role of RBPs in driving plant growth and vascular development, modulating processes such as the translation of key mRNAs involved in phloem differentiation and vascular pattern formation.

4. CRISPR- Cas in RBPs research: Unlocking new potentials and insights

CRISPR-Cas engineering has significantly improved the capacity to analyze and regulate the functions of RNA-binding proteins (RBPs) by precisely targeting post-transcriptional regulatory mechanisms [305]. Recent advancements in CRISPR/Cas9-based genome engineering in plants allow for the creation of both single and multiple functional knock-out mutants across various plant species [306,307]. This technology has facilitated the study of SR protein functions in crop species [308]. The CRISPR/Cas9 system allows the design of single guide-RNA molecules target targeting specific genomic sites to generate functional knockouts and different protein variants. It also allows precise manipulation of splice sites, including insertion, deletion, and modification of constitutive and alternative splice sites. This capability dramatically aids in studying the effects of these sequences on splicing patterns and splice isoform levels. For example, Kang et al. [309] utilized an adenine base editor fused to dCas9 to edit a 3′ acceptor site, resulting in the mis-splicing of phytoene desaturase (PDS3) pre-mRNA. Such research lays the base for engineering plants with optimized splice variants to enhance their performance under adverse environmental conditions.

Extensive research is underway to explore using CRISPR/Cas13 systems for various RNA engineering applications. One notable application involves manipulating alternative splicing by combining dCas13 (dead Cas13) with specific SR proteins [310]. CRISPR/Cas13 as an RNA-targeting complex, carrying an SR protein domain to achieve specific splicing outcomes. However, there have been no proof-of-concept studies by Konermann et al. [311] showing that dCas13d can be used to perturb splice isoforms in a targeted manner. CRISPR/Cas9 technology was used in another application to generate *RBP45D* knockout lines (rbp-ko). RNA-Seq analysis revealed that FLC mRNA levels were upregulated, and several loci, including FLM, were differentially spliced. As a result, the loss of *RBP45D* delayed flowering [312]. Similarly, in *S. lycopersicum*, *RZ1A-Like (RZ1AL)* plays a significant role in fruit ripening. Knockout of *RZ1AL* using CRISPR/Cas9 technology reduced fruit lycopene content and weight, underscoring its importance in regulating carotenoid biosynthesis and metabolism during fruit development [286]. Furthermore, an incomplete dominant large grain (Lgg) mutant was identified in nDart1-tagged lines of Koshihikari rice. By combining transposon display analysis of Lgg and Lgg-type F2 plants with CRISPR/Cas9-mediated knockout and overexpression studies, researchers determined that the gene responsible for the prominent grain phenotype is a putative RBP with two RRMs [267]. CRISPR technology has also been utilized to explore post-transcriptional regulation in plants. An example of this is the RNA proximity labeling (RPL) technique, which employs a fusion of endonuclease-deficient CRISPR-Cas protein (dCas13b) with engineered ascorbate peroxidase (APEX2) to identify RNA-proximal proteins in vivo via proximity-based biotinylation. This approach has revealed novel RNA-protein interactions, offering valuable insights into the regulatory networks that govern plant gene expression [313,315]. An RNA-binding protein called *EARLY HEADING DATE 6 (EHD6)*, which contains an RRM domain, interacts with YTH07 to regulate the heading date in rice, independent of light and temperature conditions. To demonstrate the importance of the EHD6-YTH07 interaction, yth07 knockout lines were created using CRISPR-Cas9 editing. Two yth07 loss-of-function mutants showed prolonged flowering under both non-long day (NLD) and non-short day (NSD) conditions, suggesting that YTH07, like *EHD6*, promotes flowering [314]. Therefore, this research enhances our comprehension of the intricate interactions between RNA-binding proteins and their involvement in plant development.

RS2Z35 and *RS2Z36*, members of the RS2Z subfamily, bind to HSFA2 mRNA and enhance intron retention. Through phenotypic and transcriptome analyses of single and double rs2z CRISPR mutants, along with precise iCLIP studies using UV cross-linking and immunoprecipitation in tomato leaves, it has been demonstrated that *RS2Z35* and *RS2Z36* play essential roles in RNA splicing processes and contribute significantly to thermotolerance. Their regulatory functions are dependent on and independent of HSFA2 [84]. These advancements in CRISPR-mediated genome engineering highlight its significant potential in plant biotechnology. By allowing precise and efficient genome manipulation, CRISPR technology not only deepens our understanding of complex genetic traits but also speeds up the development of crops with enhanced traits, such as higher yields, improved disease resistance, and greater stress tolerance.

5. Conclusion and future perspective

The regulation of RNA-binding proteins is a complex and dynamic process crucial for the proper functioning of cellular RNA metabolism. Through various mechanisms such as post-transcriptional modifications, RNA recognition motifs, alternative splicing, and interactions with other

proteins and signaling pathways, RBPs exert precise control over the fate of RNA molecules. RRBPs are essential for plants to adjust to diverse environmental conditions, governing critical processes, including pre-mRNA splicing, RNA export, RNA stability, polyadenylation, and chromatin modifications. Despite an extensive understanding of RBP roles in other organisms, their importance in plant biology remains only partly elucidated. Future research should focus on utilizing RBPs as potential targets to deepen our understanding of their substrate recognition and regulation of RNA metabolism. This approach could lead to crops that can withstand stress by concentrating on the genetic and epigenetic processes during both biotic and abiotic stresses. These factors initiate post-translational modifications and interactions, significantly influencing how proteins and RNA engage with each other, impacting RNA's function from its genesis to its degradation. Understanding these intricate regulatory mechanisms is crucial for and unraveling the detailed control of gene expression. The ability of these proteins to bind to RNA sequences and structures allows for meticulous regulation of the splicing process, adapted to specific contexts. Although the significance of RBPs in plants is currently being explored, there are still unanswered questions regarding their essential roles and capabilities.

RBPs are essential for post-transcriptional RNA regulation in plants. Most of the research has primarily concentrated on model plants, with the role of RBPs in non-model crop plants remaining largely unexplored. Still, research on these proteins often lacks a comprehensive experimental investigation to fully understand their role in regulating the organism. Bridging this knowledge gap is essential for aligning plant RBP research with the broader insights gained in other metazoans. Despite significant progress in genome biology enhancing our understanding of plant RBPs and a growing number of experiments aimed at identifying these proteins, much remains to be discovered. This includes the specificity of RBPs for their targets, identifying motif structures within novel or non-canonical RBDs, the critical regulators of RBPs during stress responses, and the specific functions of individual RBPs. Most plant RBPs have been identified through sequence similarity to known RNA-binding domains. However, many of these proteins' exact molecular functions and in vivo targets, are still unclear. Despite significant advances in genome biology and increased efforts in RBP identification, there is still much to uncover about plant RBPs. Key areas needing attention are the precision of RBPs' target recognition, the identification of unique or unconventional RNA-binding domain motifs, the factors affecting RBPs under stress, and the distinct roles of each RBP.

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CRediT authorship contribution statement

Shazia Rehman: Writing – original draft, Formal analysis. **Saraj Bahadur:** Writing – review & editing, Software. **Wei Xia:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Investigation, Funding acquisition, Data curation, Conceptualization. **Chen Runan:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation. **Maroof Ali:** Writing – review & editing, Visualization. **Zainab Maqbool:** Writing – review & editing, Resources, Methodology, Formal analysis.

Declaration of competing interest

We, all authors have no conflict of interest to declare.

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