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Molecular Dissection of Cold Response Pathways in Adzuki Bean

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Abstract Adzuki beans (*Vigna angularis*), as an important edible legume crop, have a wide cultivation base and nutritional value in East Asia. However, during early spring or high-latitude planting, it often suffers from low-temperature stress, which seriously affects seed germination, seedling growth and yield formation. To deeply analyze the response mechanism of adzuki beans to low-temperature stress, this study systematically explored the key regulatory networks of their cold response pathways at the molecular level, and sorted out the low-temperature perception and initial signal transduction mechanisms of adzuki beans, including the dynamic changes of early signal molecules such as calcium signaling (Ca^{2+}), reactive oxygen species (ROS), and nitric oxide (NO). Focusing on the classic ICE-CBF-COR pathway, the expression characteristics of transcription factors such as CBF/DREB, MYB, and bZIP and their regulatory effects on downstream cold resistance genes were analyzed. Further, the epigenetic mechanisms such as DNA methylation and histone modification, as well as the regulatory roles of miRNA and lncRNA in the cold response of adzuki beans were explored. In this study, through the analysis of actual cases, multiple candidate genes with significant differential expression under low-temperature conditions were identified and verified. Combined with qRT-PCR and heterologous overexpression experiments, their potential functions in enhancing cold resistance were revealed. This study provides theoretical support for a deeper understanding of the complex molecular mechanism of adzuki beans' low-temperature response, and also offers key genetic resources and technical foundations for breeding cold-resistant and high-yield varieties.

Keywords Adzuki beans; Low-temperature stress; Signal transduction; Transcriptional regulation; Cold-resistant breeding

1 Introduction

Adzuki beans (*Vigna angularis*), a leguminous crop, have long been widely cultivated in many regions due to their high nutritional value and good economic returns. But problems also arise, especially when it encounters low temperatures during the seedling stage or flowering period, its performance is very likely to "fail". When cold air comes, not only is growth hindered, but a series of physiological disorders may also occur within the plants, such as oxidative damage and metabolic abnormalities, and the yield is also affected. For those planting areas that frequently encounter low-temperature weather, this is undoubtedly a big problem (Xiang et al., 2024). If there are no appropriate cold resistance measures, farmers' investment is likely to fail to yield the expected returns and may even affect the overall stability of regional grain.

Regarding how plants respond to cold stress, research has actually revealed many mechanisms, and they seem more complex than imagined. For example, there is a type of signaling pathway called ICE-CBF-COR that is activated by low temperature, thereby driving the expression of a series of genes related to cold resistance (Wang et al., 2024b). In addition, measures such as adjusting the stability of the film and activating the antioxidant system are also ways that plants themselves use to buffer cold damage. In the experiment on adzuki beans, some people attempted to spray exogenous abolic acid (ABA), and it was found that this could enhance the activity of antioxidant enzymes and also reduce the yield loss caused by low temperatures. This also reminds us once again that hormone regulation may be an important part of plants' coping with cold stress. Not only adzuki beans, but also similar mechanisms have emerged in model plants and other crops, including epigenetic regulation and the participation of certain specific stress genes. It can be seen that there is indeed more than one way for plants to cope.

This study will systematically analyze the molecular pathways of the cold resistance response of adzuki beans, review the physiological and biochemical effects of cold stress, and then explore the latest research results on the unique gene regulation, signal network and defense mechanism of adzuki beans, identify key molecular regulatory factors, clarify their roles in cold resistance adaptation, and propose strategies for breeding or biotechnology improvement. By deepening the understanding of the cold resistance response pathway, this study has scientific significance for breeding cold-resistant adzuki bean varieties and is conducive to conducting more extensive research on crop stress biology.

2 Cold Perception and Initial Signal Transduction Mechanisms in Adzuki Bean

2.1 Perception of low temperature through membrane fluidity changes and cold sensors

When the temperature drops sharply, plant cells do not immediately activate their response through a certain "cold sensor". More commonly, the plasma membranes of adzuki beans and other plants first become less flexible - this step of change can quickly be captured by the protein or lipid signal chains on the membrane. In Arabidopsis thaliana, studies have found that low temperatures activate diacylglycerol kinase (DGK), which then converts diacylglycerol into phosphatidic acid. Such molecules act as "middlemen" in signal transduction (Wei et al., 2021). Although it is not yet fully clarified which "receptors" in adzuki beans are dominant in the response, from a conservative perspective, the mechanism is likely to be similar.

2.2 Activation and regulation of calcium signaling (Ca^{2+}) under cold stimuli

Hardly any cold stress response skips the calcium signal step. In plants such as adzuki beans, when the temperature drops, calcium ions will rapidly flood into the cytoplasm, which is one of the earliest signals of the cold response. This signal does not remain on the surface but is "read" by calcium-binding proteins such as calmodulin or CDPK and continues to be transmitted downward (Figure 1) (Ding et al., 2022; Yin et al., 2023). Research on model plants and other leguminous plants also points to a consensus: Ca^{2+} not only regulates the expression of cold-related genes but may also act as a "switch" for other adaptive mechanisms. Adzuki beans themselves also carry *GLR* genes, which means they are not "outsiders" in terms of calcium flux sensing.

2.3 Roles of reactive oxygen species (ROS) and nitric oxide (NO) in early signaling events

When the weather gets cold, calcium ions alone are not enough to make it lively. Many plants, Arabidopsis thaliana is a typical example, will simultaneously experience a wave of ROS and NO. Although they sound like "harmful elements", in fact, these two are the important "megaphones" in the early signals. With the help of NADPH oxidase, ROS production activates cold-related transcription factors and further strengthens Ca^{2+} signaling (Wei et al., 2021). Meanwhile, the emergence of NO is no accident. Together with ROS, it regulates gene expression, protein activity, and even the REDOX state of cells. It was the collaborative efforts of these initial small molecules that truly initiated the "first act" of the cold response of adzuki beans.

3 Transcriptional Regulation and Core Cold-Responsive Pathways

3.1 Activation and regulatory mechanisms of CBF/DREB transcription factors

When cold stimulation is first sensed, transcription factors such as CBF/DREB are quickly activated. They are among the first batch of regulatory elements to appear in the plant's cold response. Their goal is clear - to lock onto the DRE/CRT sequence in the promoter of the *COR* gene and initiate downstream expression (Abdullah et al., 2022). These activated *COR* genes guide the synthesis of some antifreeze proteins and osmotic regulatory substances, which help maintain cell stability and antifreeze performance. However, this pathway does not operate in isolation. Most of it belongs to the ABA-independent pathway, and its regulatory mechanism does not rely on abscisic acid. However, the expression level of CBF itself is not always constant and can also be affected by post-transcriptional and even post-translational modifications. That is to say, plants do not simply make the CBF work, but rhythmically "regulate the regulatory factors" to cope with different degrees of low-temperature stress (Wang et al., 2024a).

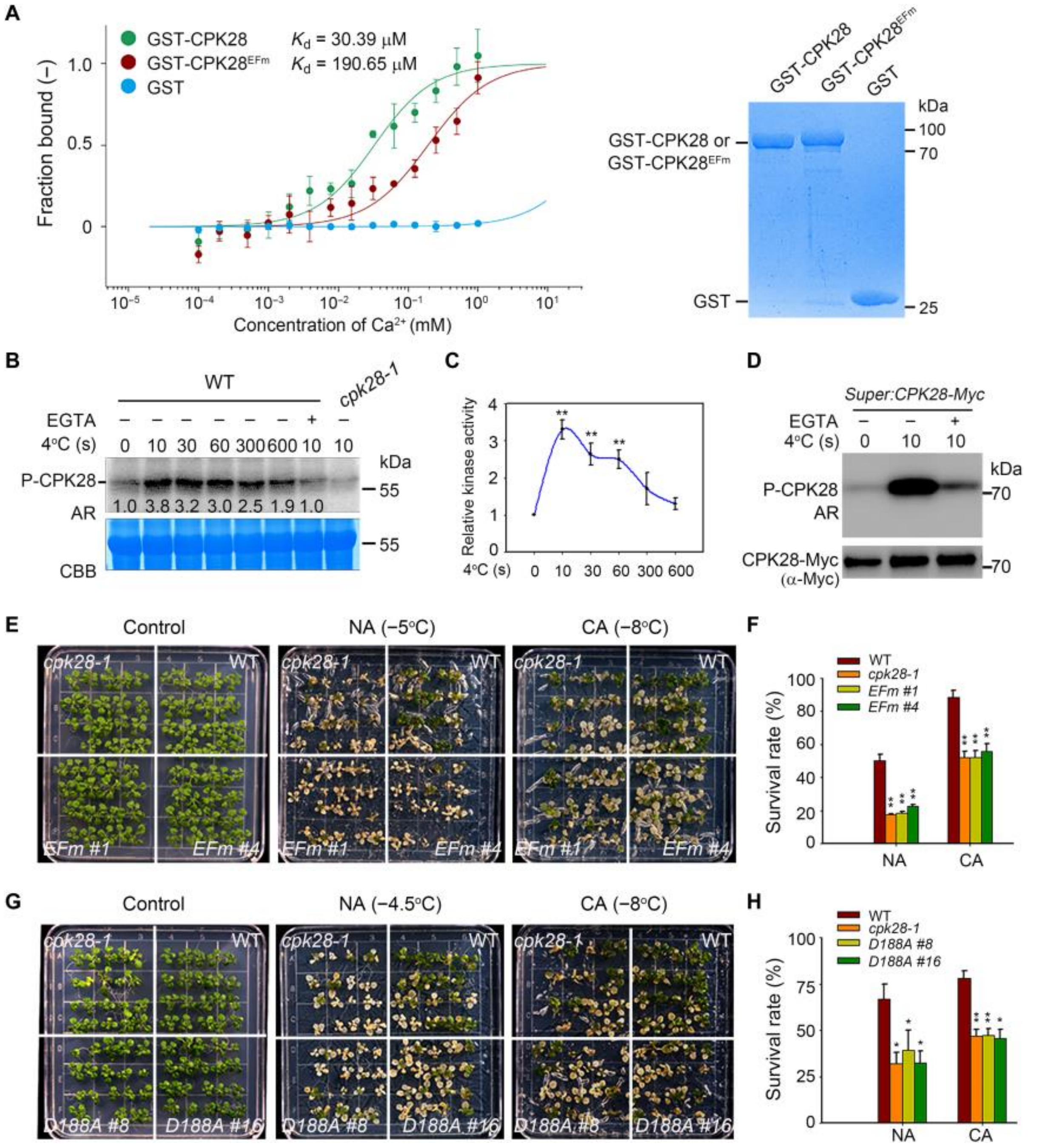

Figure 1 The Ca^{2+}-dependent activation of CPK28 is required for freezing tolerance (Adopted from Ding et al., 2022)

Image caption: (A) Microscale thermophoresis (MST) assay showing the Ca^{2+}-binding affinity of CPK28 and CPK28^{EFm}. Quantification is shown in the left; recombinant proteins were stained by CBB (right). Data are means ± SD of three technical replicates. Similar results were obtained from three independent experiments. (B to D) In-gel kinase assays showing CPK28 activation in response to cold. The 14-day-old wild-type plants (B and C) or *Super:CPK28-Myc* plants (D) were treated at 4°C for the time indicated without EGTA or for 10 s after pretreatment with 25 mM EGTA for 4 hours, and total proteins (B) or immunoprecipitated CPK28-Myc with anti-Myc agarose beads (D) were subjected to in-gel kinase assay. GST-BIK1^{K105E} was used as substrate. cpk28-1 mutant treated at 4 °C for 10 s was used as controls (B). Autoradiograph (AR) and CBB staining (B) or CPK28-Myc (D) are shown in the top and bottom, respectively. Relative kinase activity is shown in (C), with the intensity at 0 s set to 1.0. Data are means ± SEM of three independent experiments ($^{**}P < 0.01$, Student's t test). (E to H) Freezing phenotypes (E and G) and survival rates (F and H) of wild-type, *cpk28-1*, *cpk28-1 CPK28pro:CPK28^{EFm}* (*EFm #1* and *#4*), and *cpk28-1 CPK28pro:CPK28^{D188A}* (*D188A #8* and *#16*) seedlings. In (F) and (H), data are means ± SEM of three independent experiments, each with three technical replicates ($^{*}P < 0.05$ and $^{**}P < 0.01$, Student's t test) (Adopted from Ding et al., 2022)

3.2 Potential regulatory network of the ICE-CBF-COR pathway in adzuki bean

The well-known cold regulation module in Arabidopsis thaliana - the ICE-CBF-COR pathway - may not be "groundless" in adzuki beans either. At the ICE beginning, once a cold signal is introduced, it is responsible for activating the expression of CBF. The CBF will continue to drive the work of the *COR* gene. This series of "relays" will enable cells to enhance antioxidant capacity, stabilize membrane structure, and even reduce the damage caused by dehydration in a low-temperature environment (Ding et al., 2022). However, the performance of the ICE protein itself is not static. It is controlled by multiple kinases and ubiquitin systems. That is to say, the time and intensity of its "activation" also vary in response to the duration of external cold stimulation. Although our understanding of this system in adzuki beans is not yet deep enough, leguminous plants generally possess similar regulatory potential. Current studies have provided some evidence for its existence (Kidokoro et al., 2022).

3.3 Other cold-responsive transcription factors (e.g., MYB, bZIP, NAC) and their functions

CBF is indeed a "leading player", but it is not the only "trader". Transcription factor families like MYB, bZIP and NAC are also involved in different stages of cold adaptation to varying degrees. MYB, especially those members that can collaborate with bHLH proteins, often participate in the regulation of antioxidant substances such as anthocyanins (Mehrotra et al., 2020). The bZIP family, on the other hand, is more involved in the restart of transcription programs or the establishment of stress memories. NAC transcription factors have received the most attention in recent years. They can not only independently regulate cold-induced genes but also may "cross forces" with the CBF pathway, making them increasingly important in regulating cold responses (Diao et al., 2020; Abdullah et al., 2022). Overall, these "supporting roles" may not play as concentrated a role as CBF, but within the entire network, their regulatory "methods" are more diverse.

4 Epigenetic and Non-Coding RNA Regulatory Mechanisms

4.1 Regulation of cold-responsive genes by DNA methylation and histone modifications

Not all genes will react immediately in a cold environment. Sometimes, plants need a more "cautious" regulatory approach to determine when genes are turned on and off. This "switch" mechanism involves DNA methylation and histone modification. In the study of Arabidopsis thaliana, long non-coding Rnas (lncrnas) such as SVALKA recruit multi-comb complex PRC2 to demethylate histones of cold-response genes like *CBF3*, resulting in tighter chromatin and greater difficulty in transcription (Kiger and Schroeder, 2024). However, this regulation is not static. Under prolonged low temperatures, it is actually dynamically adjusted - neither keeping the cold response on all the time nor turning it off too early. This mechanism is very likely to have a similar "universal version" in leguminous plants, such as adzuki beans.

4.2 Post-transcriptional regulation mediated by miRNAs under cold stress

Not all cold stress responses occur at the "starting point" of gene expression. The "behind-the-scenes role" of miRNA emerges in the post-transcriptional stage. It does not activate genes but selectively "silences" some mRNA that has already been produced. Cold response mirnas such as miR397, miR408, miR394, which have long been discovered in Arabidopsis thaliana, as well as miR156, miR319 and miR528 in rice, have different functions - some affect hormone signaling, some regulate antioxidation, and some intervene in metabolism (Huo et al., 2021). High-throughput sequencing has gradually clarified these regulatory networks. Not only in model plants, but also in legumes and grains, a large number of cold-related mirnas have been discovered. Although adzuki beans have received less research, based on the existing data, they may also be equipped with a similar miRNA regulatory system.

4.3 Potential roles of lncRNAs and circRNAs in cold adaptation

Long non-coding Rnas (lncrnas) and circular Rnas (circrnas) may not sound like the main characters, but at low temperatures, they could be the "tuners" maintaining system stability. Take SVALKA as an example. It is no mere decoration in Arabidopsis thaliana - it regulates the activity of CBF-like transcription factors by interfering with transcription, recruiting chromatin modification complexes, and even influencing miRNA pathways. Furthermore, lncRNA can also act as ceRNA to competitively "adsorb" miRNA, indirectly allowing cold response genes to "escape silencing". This phenomenon has also been observed in wheat and grapevines (Lu et al., 2020). In contrast, circRNA research has not kept pace yet, but some data have suggested that they may also function in the form of "miRNA sponges" (Wang et al., 2019). Overall, although lncRNA and circRNA are not as "conspicuous" as mRNA, it might be they that maintain the response rhythm of adzuki beans behind the scenes during cold adaptation.

5 Case Study: Identification and Functional Validation of Key Cold-Responsive Genes

5.1 RNA-Seq-based analysis of adzuki bean under cold stress conditions

Not all transcriptome studies were initially aimed at low temperatures. Gene families involved in RNA silencing, such as DCL, AGO and RDR, were actually first systematically organized during the study of drought or disease stress (Li et al., 2023). However, it was precisely these studies that provided methods and ideas, and also enabled us to later identify some differentially expressed genes and regulatory networks more quickly under the cold stress conditions of adzuki beans using RNA-Seq. Looking back now, these classified gene families might also be an indispensable part of the cold adaptation mechanism.

5.2 qRT-PCR validation and expression profiling of candidate genes

The results of RNA-Seq cannot be used directly and need to be further confirmed by qRT-PCR. In the case of adzuki beans, previous studies have analyzed the expression patterns of stress-related genes such as *DCL*, *AGO*, and *RDR* using qRT-PCR and found that their expression changes under adverse stress were indeed quite obvious (Figure 2) (Li et al., 2023). However, to be more precise, it still depends on whether the reference genes are well selected. Some studies specifically selected and verified reference genes applicable to adzuki beans, so that expression profiling analysis under different adverse conditions (including low temperature) would not be biased (Imoto et al., 2022).

5.3 Functional analysis in heterologous systems

Not all genes can be verified in adzuki beans before discussing their functions. At this point, model plants need to be used for assistance. Laboratory "veterans" like Arabidopsis thaliana and tobacco are often used in functional verification to overexpress candidate genes to see if they can enhance stress tolerance. The previously mentioned *DCL*, *AGO* and *RDR* genes, their related miRNA targets and feedback regulatory circuits have obtained preliminary clues in adzuki beans, and also provide good candidates for subsequent functional verification in these heterologous systems (Li et al., 2023).

6 Breeding Potential of Cold-Responsive Genes in Adzuki Bean

6.1 Development of molecular markers and MAS strategies for cold tolerance

Nowadays, in breeding, relying on intuition or field experience is no longer sufficient. Especially when it comes to complex traits such as cold resistance, traditional methods are often inefficient and time-consuming. As a result, breeders have increasingly relied on molecular markers to assist in screening (MAS). Of course, this is not something that can be accomplished overnight - a reliable high-density genetic map is needed first, along with QTL mapping, to provide technical support. For crops like adzuki beans, some QTLS related to abiotic stress have been identified. It is precisely these fundamental studies that have made it possible for MAS to be applied in cold-resistant breeding (Jha et al., 2016; Dwivedi et al., 2023).

6.2 Association studies between cold-responsive genes and QTLs

Not all genes can be associated with low-temperature response. To figure out who is related to whom, QTL analysis and association plotting are required. In recent years, researchers have identified some QTL regions related to stress such as cold resistance and drought, among which there are many hotspots related to domesticated traits. Some candidate genes were also proposed and entered the subsequent functional verification process (Wang et al., 2025). From a practical perspective, this approach of integrating multiple stress-response traits helps enhance the environmental adaptability of varieties, not only focusing on cold but also coping with other stresses simultaneously.

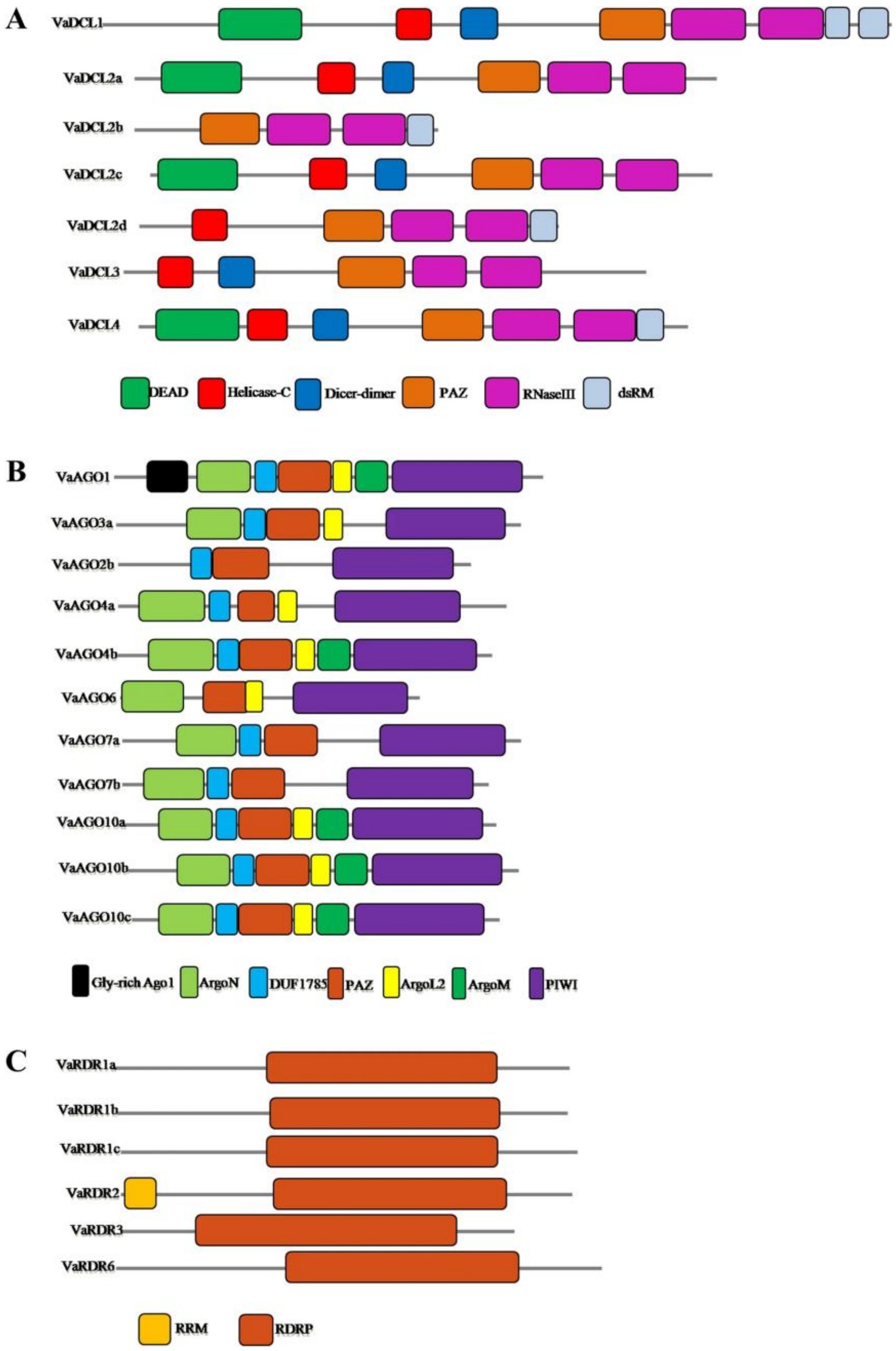

Figure 2 Domain compositions of adzuki bean DCL (A), AGO (B), and RDR (C) protein sequences. Domains are indicated as boxes in various colors. The diagrams were drawn to scale (Adopted from Li et al., 2023)

6.3 Identification of cold-tolerant germplasm and breeding strategies for resilient varieties

Not every adzuki bean variety is equally resilient to cold weather. The screening results of a large number of germplasm resources show that the performance of different varieties varies greatly, whether in the germination stage or the seedling stage. For instance, among 384 resources, only 31 demonstrated relatively outstanding cold resistance during the germination stage, while several species like GI-34, JN95-0, and E0064 were equally stable during the seedling stage. These well-performing materials are of great significance to breeding projects that aim to ensure both yield and enhance cold resistance. In addition, some studies have also found that exogenous spraying of ABA can help crops maintain a stable state at low temperatures. Although it is not a fundamental solution, it can reduce some losses at critical points and can be regarded as a practical supplementary path (Xiang et al., 2024).

7 Conclusion and Future Perspectives

How do adzuki beans "identify" coldness? In fact, this matter is quite complicated. At first, the fluidity of the membrane changes, followed by an increase in calcium ion concentration and a rapid accumulation of reactive oxygen species (ROS). All these are like alarms, immediately sending out the low-temperature signal. Then, a batch of key transcription factors will be activated, such as CBF/DREB, MYB, bZIP and NAC, which act like switches to control a long string of genes related to cold resistance. Further down, epigenetic regulation and non-coding Rnas also step in to participate in fine-tuning. The existing QTL mapping and transcriptome data have also enabled us to identify several genes and regulatory networks that may be closely related to cold tolerance adaptation.

However, to be fair, although the research has made considerable progress, there are still many blind spots. A very realistic problem is that the omics data of Xiaodou itself is currently not systematic and complete enough, especially the information on some specific genes and regulatory factors is relatively scarce. Moreover, the genetic differences among various varieties, coupled with environmental interference, make it somewhat difficult for us to simply apply the research results of model species to adzuki beans without any modification. Furthermore, many of the proposed candidate genes have not yet undergone functional verification, especially those involving secondary metabolites such as flavonoids, whose exact roles in cold resistance remain unclear to this day.

For future research, several directions need to be advanced simultaneously: First, it is necessary to continue to expand genetic resources, screen more red bean germplasms, and not neglect wild relatives either. Maybe new genes can be discovered. Second, omics analysis should be conducted more deeply, combining genomic, transcriptomic, metabolomic and more detailed phenotypic data, which can accelerate the identification of key pathways. Thirdly, it's time for gene editing tools to come in handy. Technologies like CRISPR/Cas can precisely identify certain target genes or regulatory sites. Fourth, it is necessary to enable marker-assisted selection and genomic selection to truly play a role in breeding and enhance efficiency. Finally, multi-omics integration should not merely be about making diagrams; it is necessary to truly construct networks using systems biology methods. Only in this way can the molecular mechanisms explored in the laboratory be truly transformed into practical achievements in breeding. For adzuki beans, adapting to climate change and enhancing cold resistance ultimately still depends on the coordinated efforts of these several aspects.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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