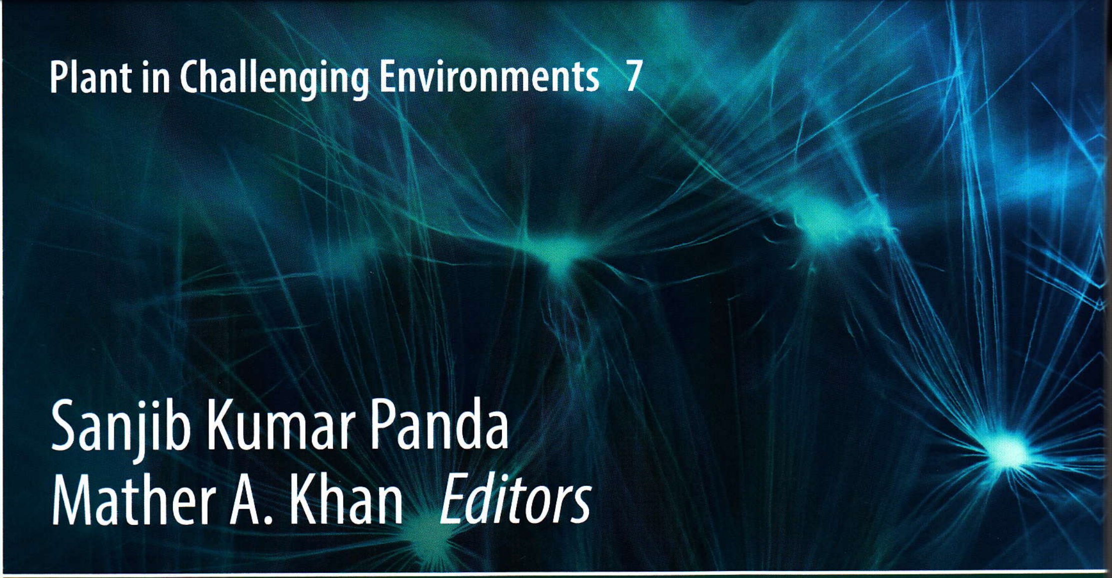

Plant in Challenging Environments 7

Sanjib Kumar Panda
Mather A. Khan *Editors*

Plant Functional Genomics for Abiotic Stress Resilience

Springer

Plant in Challenging Environments

Volume 7

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ISSN 2730-6194 ISSN 2730-6208 (electronic)
Plant in Challenging Environments
ISBN 978-3-032-01703-1 ISBN 978-3-032-01704-8 (eBook)
https://doi.org/10.1007/978-3-032-01704-8

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Contents

Chapter 9

Conservation and Diversification of the Cold Stress Response in Higher Plants

Arabindu Debbarma, Rakhi Chaturvedi, Kyonoshin Maruyama, and Yoshiharu Y. Yamamoto

Abstract Cold stress poses a significant challenge to plant development, leading to significant reductions in crop yield. While a few plants that are temperate, exemplified by *Arabidopsis thaliana*, exhibit internal adjustments to maintain metabolic machinery during cold temperatures through a procedure called "cold acclimation", plants that are tropical or subtropical, like rice, show sensitivity to chilling stress. Temperate plants must first undergo cold acclimation, which involves to be exposed to low, freezing temperatures in order to prevent damage during subsequent freezing stress and to ensure the plant's general health under low temperatures. Intricate physiological, biochemical, and molecular systems have been developed by plants to detect and react to low temperatures. Notably, two essential elements of this response are cytoskeletal rearrangement and membrane modifications. Calcium-binding proteins and calcium-dependent protein kinases are activated by the little increase in cytosolic calcium levels, which adds to the complex network of regulation during low-temperature stress. Furthermore, the plant response to cold stress is greatly affected by epigenetic regulation. This review compiles the most recent findings and advancements in our understanding of the tactics used by plants to

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S. K. Panda, M. A. Khan (eds.), *Plant Functional Genomics for Abiotic Stress Resilience*, Plant in Challenging Environments 7,
https://doi.org/10.1007/978-3-032-01704-8_9

withstand low temperatures. By examining the conservation and diversification of the cold stress response in higher plants, the main aim of the review is to provide valuable insights into the intricate molecular networks governing plant adaptation to cold environments. The integration of physiological, biochemical, and molecular perspectives enhances our understanding of the adaptive mechanisms that contribute to plant resilience under challenging low-temperature conditions.

Keywords Cold acclimation · Conservation · Diversification · Epigenetics · Freezing stress

9.1 Introduction

Abiotic stressors that negatively impact growth and productivity includes heat and cold stress (CS), drought, heavy metal toxicity, nutrient shortage, acidity and salinity of the soil, and structure, characteristics, biochemical, and genetics changes in plants (Imran et al. 2021). Temperature effects on the growth of plants differs between species or populations, since their reactions to different temperature ranges vary widely (Shi and Yang 2014). Certain plants native to tropical or subtropical regions, accustomed to warmer temperatures, might experience cold injuries or stress when exposed to cooler temperatures below 15 °C. Conversely, Antarctic algae, adapted to extremely cold environments, might exhibit signs of heat stress or physiological disruption when temperatures rise above 5 °C (Guy et al. 1985).

CS is the substantial abiotic stresses that significantly affect crop productivity as well as the geographic distribution of many plant species. It can inflict fatal harm, significantly impacting their productivity and survival rates. Low-temperature stress impacts various facets of plant life, encompassing germination, growth, development, and reproductive processes. In general, plants face chilling (0–15 °C) and freezing (>0 °C) as the most common CS (Albertos et al. 2019; Pan et al. 2020). In temperate zones, rice is especially susceptible to chilling stress, especially in high-elevation areas and at high latitudes. Rice seedlings that are exposed for more than four days to temperatures below freezing experience reduced germination, slowed growth, and occasionally even death. Furthermore, during times of chilling stress, researchers have observed a widespread outbreak of rice blast disease, resulting in significant losses in rice production. Sensitive plants exposed to chilling injury often exhibit observable signs such as chlorosis (yellowing of leaves), rigidity or stiffness in seedlings, wilting, and even the occasional seedling death. These observable phenotypes are helpful markers for differentiating between plant varieties that are sensitive and tolerance to chilling (Xie et al. 2023).

To acclimate amidst profoundly challenging environmental circumstances plants have evolved efficient survival mechanisms. Numerous temperate plants, including *Arabidopsis thaliana*, rapeseed, wheat, and rye, have evolved mechanisms to sense and react to freezing stress through a mechanism called cold acclimation. Cold acclimation necessitates low exposure, but not subject to freezing temperatures, which triggers the plant capability to cope with subsequent CS. This adaptive mechanism helps the plant maintain its overall health and functionality despite the unfavourable low-temperature conditions (Huang et al. 2017). Perennial plants, such as trees, perceive seasonal changes by monitoring alterations in both photoperiod (day length) and temperature through the year. These plants go from active growth to dormant phases and develop frost resistance for cold hardiness in response to signals from variations in day length and temperature. In temperate climates, this transformation is essential for woody plants to survive winter conditions. Perennial plants have morphological and physiological characteristics that enable them to synchronize with climatic rhythms, which helps them survive in harsh cold environments, unlike annual herbaceous plants (Sharma et al. 2022).

Since the initial discovery of cold tolerance genes by Guy et al. (1985) and their naming as *cold-regulated* (COR) genes (Hassan et al. 2021), substantial advancements have occurred in comprehending the molecular mechanisms underlying plants' reactions to CS. Recent studies have isolated and characterized~~,~~ numerous genes that respond to freezing stress, highlighting their importance in both chill tolerance and cold acclimation processes. *The CBF/DREB1* pathway is among the most well-studied and important cold signalling pathways out of several others (Lv et al. 2020). Plant responses to stress are largely dependent on regulatory genes, particularly transcription factors (TFs). By inducing the expression of useful genes, their activation either directly or indirectly regulates the signal transduction network and genes that respond to stress. Osmo-regulators and anti-freeze proteins are direct regulators while proteins like chaperones, functional proteins, TFs, and kinases are indirect regulators (Miura and Furumoto 2013).

In order to select CS resistant crop cultivars, the availability of molecular markers assist quick screening, bypassing the need to wait for observable phenotypic changes. Compared to other stresses, the reactions of plants to CS are complex, what makes difficult to increase crop tolerance to cold. Nonetheless, over the previous 20 years, efforts have led to the creation of transgenic crop lines, exhibiting enhanced CS tolerance (Jiang et al. 2017). To achieve improved outcomes, it is crucial to utilize appropriate tools and genotypes that surpass existing varieties and are accessible to farmers (Aslam et al. 2022). This review covers emerging research areas, technological advancements, and tools for studying plant cold tolerance additionally to reviewing various genes and mechanisms participating in higher plants' adaptive responses to CS.

9.2 Cold Stress Resilience in Plants: Signalling Pathways, Small Molecules, Hormonal Dynamics, and Gene Regulation

9.2.1 *Cellular Adaptation and Membrane Dynamics in Cold Stress Resilience*

Biological membranes are essential for cell protection, homeostasis, and metabolism. The cell membranes composed of lipids, sterols, and proteins, collaborate and actively participate in cellular metabolism (Cacas et al. 2012). The cell membranes adaptability is frequently hinged due to cold temperature resilience. Metabolite homeostasis re-establishing occurs due to compositional changes in both lipids and membrane protein and represent a process whereby cells detect cold temperatures. The alterations induced by low temperatures in membrane physical conformation primarily increased unsaturated fatty acids enhancing membrane liquidity and solidity. This adaptation enables cells to mechanically adjust to the cold environment (Khodakovskaya et al. 2006). Proteins and membrane lipids are stabilized by the presence of higher amount of sugars, nitrogen compounds, and proteins to preserving membrane integrity in cold acclimation (Jiang et al. 2021).

When the plasma membrane stiffens during cold acclimation, it influences ion concentration and metabolite transport from apoplasts, endo-membranes, and organelles. This starts the cold signaling cascade downstream. Plants sense their surroundings and convert the signal into subsequent biological reactions by decreasing the fluidity of their membranes. This affects the cellular activities associated with the membranes. Calcium channels, a transmembrane protein complex, is primary pathway for calcium ions to enter cells, that are vital sensors for abiotic stress. Plants sense CS and then a complex cascade of signal transduction processes in the nucleus and cytosol begins. For intracellular signaling secondary messengers such as nitric oxide (NO), reactive oxygen species (ROS), and Ca^{2+} are necessary as well as for cell-to-cell communication during these events. The regulation of *CBF/DREB1* pathway, in response to CS, causes modifications in post-transcriptional and post-translational modifications and triggers subsequent downstream reactions (Liu et al. 2019).

The freezing process is initiated by accumulation of water molecules in plant cells, which causes stable ice nuclei at freezing temperatures. The process of ice formation starts at the nucleation site which is formed due to the assimilate of microscopic ice nuclei by formation of ice-nucleating proteins (INPs). These sites help water molecules align correctly, which in turn encourages the creation of extracellular ice crystals. Lack of ice-binding proteins (IBPs), big ice crystals developed in the apoplast that has potential to physically harm plasma membranes. Cell dehydration results from an osmotic gradient caused due to ice crystallization followed by isolation of intracellular water. Cell collapse or rupture may arise from this loss of cell volume (Denais et al. 2016). Through a process unique to plants called supercooling, avoidance mechanisms lower the intracellular freezing temperature by utilizing a range of cryoprotectant molecules. These molecules help prolong or prevent the formation of extracellular ice crystals, by keeping intracellular liquids cooler than zero (Bhandari and Nayyar 2013). By using IBPs as part of its survival strategy, certain plant species have created intricate systems that reduce the freeze damage. IBPs, also known as antifreeze proteins (AFPs) or ice recrystallization inhibition (IRI) proteins, are a class of low temperature-associated proteins found in a range of cold-adapted organisms, including plants like *Ammopiptanthus nanus* and *Loliurn perenne* (Wisniewski et al. 2020). Plant IBPs able to communicate with ice crystals because of their special structural characteristics and functional traits. Therefore, they cannot grow, and water molecules are unable to exit the intracellular compartment into the extracellular space. This binding ability keeps the cell from freezing and helps to prevent it from becoming dehydrated. It has been noted that these ice-binding proteins are diverse in multiple AFPs from different plant species. For example, *Fs*AFP from weeping forsythia (*Forsythia suspensa*) has sequence similarity to dehydrin, and *Pa*AFP from Norway spruce (*Picea abies*), *Ta*IRI1-2 from winter wheat (*Triticum aestivum*), *Ba*AFP from malting barley (*Hordeum vulgare* L.) have similarity to chitinase, thaumatin-like protein, and alpha-amylase inhibitor protein, respectively (Bredow and Walker 2017).

9.2.2 Role of Small Signalling Molecules in Responses to Cold Stress Adaptation in Plants

Small signalling molecules function as pivotal regulators in various stress conditions within plants, generated upon the detection of environmental stress via signal transduction pathways (Tuteja and Sopory 2008). These molecules are important since they transmit and amplify stress signals, start cascade reactions that regulate gene expression, osmoregulation, function of antioxidant enzymes, and communicate with other signal pathways. These signalling molecules under the influence of CS orchestrate diverse actions, mediating gene regulation, adjusting osmotic balance, modulating antioxidant enzyme functions, and engaging in crosstalk with other signalling pathways (Lamers et al. 2020). Identified signalling molecules such as ROS, Ca^{2+}, NO, cyclic guanosine monophosphate (cGMP), hydrogen sulfide (H_2S), and lipid-derived signals, notably diacylglycerol (DAG), phosphatidic acid (PA), sphingolipids, and inositol triphosphate (IP3), synergistically operate through crosstalk mechanisms (Barrero-Sicilia et al. 2017).

Secondary messenger Ca^{2+} is known to participate in several biological processes in eukaryotic cells, among which cold stress response is its major role plants. A strong influx of Ca^{2+} into the cell was caused by the activation of Ca^{2+} channels by the cold signal. The sensors that are activated by Ca2+ ions include calcineurin B-like proteins (CBLs), calmodulins (CaMs), CaM-like proteins (CMLs), and Ca^{2+}-dependent protein kinases (CPKs/CDPKs). These sensors further trigger the downstream process through phosphorylation, transcriptional reprogramming, and activation of MAPKs cascade (Yuan et al. 2018). Conversely, the constitutive suppression of MPK3 and MPK6 kinase activities and proteins is due to a *MEKk1-MKK2MPK4* cascade that also contributes positively to regulating temperature response (Zhao et al. 2017a, b). CS induced plasma membrane rigidification in alfalfa and *Brassica napus* causes cytoskeletal actin rearrangement, Ca^{2+} channel induction, and a rise in cytosolic Ca^{2+} levels. These circumstances cause cold acclimation and the expression of COR genes (Chinnusamy et al. 2010; Sangwan et al. 2001)

9.2.3 Effects of Phytohormones in Response to Cold Stress in Plant

Phytohormones performed a crucial task in helping CS tolerance by intricating physiological as well as biochemical mechanisms, to foster overall growth and development of the plant. Among these, abscisic acid (ABA) is pivotal in orchestrating physiological stress responses in plants during CS (De Smet et al. 2006). Normally, plants require low levels of ABA for growth, with excess ABA regulated via its endogenous biosynthesis. However, low temperatures induce osmotic stress due to decreased water availability in plant cells, prompting increased ABA production and biosynthesis. Endogenous ABA is transported from roots to leaves, leading to its accumulation in guard cells, resulting in stomatal closure, reduced transpiration rates, and suppressed cell growth (Cotelle and Leonhardt 2019).

Elevated levels of ABA within cold-tolerant plants serve as an intracellular signal, facilitating the process of creating fresh proteins during the process of cold acclimation. Furthermore, the application of exogenous ABA can enhance CS tolerance in various plants by triggering ABA signalling pathways. These pathways induce the transcription of antioxidant enzymes that aid in scavenging ROS, thus reducing CS-induced damage. ABA's role in CS signalling is regulated via pathways independent of *CBF* (Zhang et al. 2013). Plant responses to CS can be modulated through either ABA-dependent or ABA-independent pathways (Roychoudhury et al. 2013). The most commonly reported ABA-regulated genes are the *Late Embryogenesis Abundant (LEA)* or *LEA*-like genes (Banerjee and Roychoudhury 2016). Abscisic acid responsive element (*ABRE*) is an 8 bp cis-acting element with the ACGT core sequence in the middle. The *Em1a* element (GGACACGTGGC) of the *Em* (*Early-Methionine-labelled*) gene is recognized as a potent *ABRE* (Guiltinan et al. 1990).

9.2.4 Function of ABA in Cold Stress Response

According to Xue-Xuan et al. (2010), ABA is a significant regulator of growth and development, impacting a variety of processes including leaf senescence, seed dormancy and germination, cell division, and elongation. Since it causes stomatal closure and osmolyte accumulation in plants under environmental stresses like drought and chilling stress. According to reports, ABA also serves as the primary phytohormone involved in stress signalling (Daszkowska-Golec and Szarejko 2013). ABA must be essential for cold acclimatization because of the brief rise in ABA during cold stress and the application of ABA's ability to increase freezing tolerance (Xue-Xuan et al. 2010). An effective way to combat winter temperatures is through cold stress-induced leaf senescence, which is brought on by ABA and cytokinins participates in preventing the breakdown of chlorophyll.

The ratio of ABA to cytokinins (ABA/CKs) in senescent *Iris pseudocorus* leaves increased significantly under natural conditions; this was most noticeable in November and December when ABA concentration was between 72% and 75% and CKs content was lower (Caselles et al. 2021). Higher ABA concentrations, as well as higher soluble sugar and non-structural carbon (NSC) contents, were observed in tetraploid *Fragaria moupinensis*. This suggests that ABA regulates the aggregation of NSC and soluble sugar during the species' reactions to CS. In their study, Karimi (2017) discovered that ABA can enhance total soluble protein (TSP) and polypeptide biosynthesis in unfavorable environmental circumstances. TSP then functions as a protective mechanism to maintain intracellular osmotic pressure, allowing leaf cells to minimize damage when exposed to low temperatures. All the grapevine leaves treated with ABA had higher TSP concentrations than the control leaves. It is commonly known that proteins have anti-freeze properties on cell membranes and various other cell structures.

In *Arabidopsis,* cold conditions were used to induce the expression levels of the ABA responsive transcription factors *ABF1* and *ABF4*. Huang et al. (2017) observed the expression of COR genes like *ABF1*, *CBF1*, and *LEA* is induced by both native and exogenous ABA application on bermudagrass (*Cynodon dactylon* (L), Pers.). Binding of *ABA* to *PP2C* blocks its activity, causing phosphorylate of *SnRK2* and there by activate its enzymatic activity. Subsequently, *SnRK2* controls the expression of ABA-induced genes and phosphorylates *ABF* transcription factors (Fujita et al. 2013). Earlier studies, suggests that *ABF2* is crucial for the transduction of the glucose signal and its overexpression can increase the sensitivity to ABA and glucose, which strengthens their resistance to these stresses (Kim et al. 2004).

For *ABA*-dependent transcriptional regulation, a single copy of *ABRE* is insufficient. Multiple copies of *ABREs* may exist upstream of stress-inducible genes, or *ABRE(s)* might act in conjunction with another GC-rich sequence known as the coupling element (CE) (Hobo et al. 1999; Shen et al. 1996). These *ABRE* and CE elements, when located within less than a 20 bp distance, together form an abscisic acid-responsive complex (ABRC). For instance, *CE1*, *CE3*, and motif III constitute an ABA-responsive complex in the regulation of wheat *HVA22*, *HVA1*, and *Rab16B* genes (Chakraborty and Roychoudhury 2022). Transcription factors (TFs) of the bZIP and *APELATA2* (AP2) types, and *VIVIPAROUS1 (VP1)/ABI3* a key transcriptional regulator, participate in gene expression. The bZIP TFs engage in dimer interactions with ABREs, which are "G-boxes" in promoter elements that contain ACGT (Francko et al. 2011). Transcription factors belonging to that of basic leucine zipper (bZIP) family predominantly bind to *ABREs/CEs* inside its target genes, controlling their stress-inducible expression (Sanghera et al. 2011).

9.2.5 The Function of CBF/DREB1 *Pathway in Cold Stress Response*

In CS response, the *CBF/DREB1*-dependent pathway stands out as a well-defined regulatory mechanism (Knight and Knight 2012). Previous research indicates that the CBF3/DREB1A pathway is governed by *ICE1* (*INDUCER OF CBF EXPRESSION 1*); however, recent studies came to the conclusion that ICE is not involved in *DREB1A* activation. In their research on mutant ice1-1, Kidokoro et al. (2020) have confirmed that transgene-induced DNA methylation, rather than gene activation, was the cause of DREB1A repression. Further study verifies the involvement of a circadian-clock related MYB family, *LATE ELONGATED HYPOCOTYL* (*LHY*) and *CIRCADIAN CLOCK-ASSOCIATED1* (*CCA1*) as indirect expression of *DREB1* in *Arabidopsis* during cold stress. *REVEILLE4/LHY-CCA1-Like1* (*RVE4/LCL1*) and RVE8/LCL5 belonging to MYB proteins serve as direct DREB1 expression during cold stress (Kidokoro et al. 2021). The team in their further investigation found out light-inducible and clock-regulated (LNK) proteins in cooperation with RVEs under heat and CS. Among four Arabidopsis LNK genes, LNK3 and LNK4 function in response to cold stress, which is activated through phosphorylation under the conditions (Kidokoro et al. 2023).

The DREB proteins, DREB1 and DREB2, partake in distinct signal transduction pathways that react to low temperatures and dehydration, respectively. The *DREB* family encompasses novel *DREB1* and *DREB2*-related genes, including *DREB1D/CBF4* and *DREB1F*, which respond to high-salinity treatments. Notably, *DREB1A/CBF3*, *DREB1B/CBF1*, and *DREB1C/CBF2* are specifically trigger by low-temperature stress in an ABA-independent manner (Liu et al. 1998). Research has indicated rapid accumulation of *CBF* gene transcripts within minutes of exposure to cold, with varying expression patterns among *CBF1/DREB1B*, *CBF3/DREB1A*, and *CBF2/DREB1C*. While *CBF1/DREB1B* and *CBF3/DREB1A* show swift induction within 15 min, *CBF2/DREB1C* transcripts accumulate more gradually, peaking after 2.5 h of cold exposure (Novillo et al. 2004). The promoters of these target genes often contain the *DRE/CRT* or related core motifs. The swift induction of *CBF* transcripts upon cold exposure suggests the presence of a transcription factor at normal temperatures that recognizes *CBF* promoters and triggers *CBF* expression upon exposure to cold stress (Maruyama et al. 2004).

9.2.6 Role of Circular RNAs (circRNAs) in Plant Responses to Cold Stress

The advent of high-throughput sequencing technology and advanced big data analysis has led to new findings and characterization of numerous non-protein-coding genes in plant stress responses. Noncoding RNAs, capable of interacting directly with DNA, RNA, and proteins, control the expression of genes responsive to environmental stress (Khaldun et al. 2016). Circular RNAs (circRNAs), a unique class of noncoding RNAs lacking 5′ caps or 3′ tails, have gained attention in plant research, including species like *Arabidopsis*, rice, tomato, wheat, and soybean (Chen et al. 2019).

Research studies focusing on circRNAs in plants, such as tomato and grape, have indicated their involvement in chilling response and cold resistance (Yang et al. 2020; Gao et al. 2019). Studies in soybean have highlighted the tissue-specific expression of circRNAs (Zhao et al. 2017a, b). Notably, in tomato, 163 circRNAs have been confirmed to respond to chilling injury, suggesting their potential regulatory role under low-temperature stress conditions (Zuo et al. 2016)

In a study by Wang et al. (2020a, b), 14 circRNAs were investigated in soybean, revealing that nine were upregulated and four were downregulated under stress conditions. These expression patterns align with the stress-specific expression observed in most plant circRNAs, emphasizing the potential participation of circRNAs in responses to low-temperature stress in soybean.

Figure 9.1 overviews signaling pathways activated by the cold stress. As we have seen, transcriptional regulation in plant cells is achieved by at least four distinct signaling pathways.

9.3 Conservation of Cold Stress Response Across Plant Species: Key Regulators and Transcription Factors Involved

9.3.1 CBF/DREB1*-Dependent Signalling Components Conferring Plant Cold Tolerance*

The *DRE/DREB1A*-dependent pathway is crucial for cold-inducible gene expression (Yamaguchi-Shinozaki and Shinozaki 2006). The C-repeat binding factor/dehydration-responsive element-binding protein 1 (*CBF/DREB1*) genes are swiftly activated during CS, playing vital function in plant cold acclimation, notably through the *CBF*-COR signalling pathway. These CBF proteins, acting as DNA-binding factors, specifically recognize the DNA-regulatory element *CRT/DRE* situated within the COR gene promoters, thereby regulating COR gene expression (Gilmour et al. 1998). The COR genes encompass various classes such as cold regulated, low

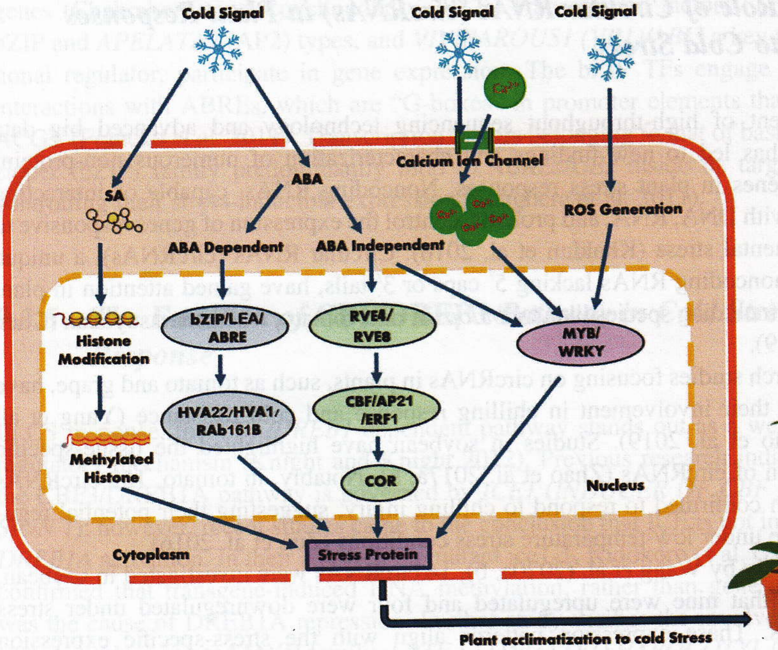

Fig. 9.1 Different mechanism of plant in response to cold stress
Salicylic acid under cold stress condition modifies through DNA methylation and downstream regulation preventing from CS. ABA also mediates the cold signal and activates ABRE-containing genes in the promoter region. There is another, ABA-independent signaling pathway activating the DREB/CBF regulon. In parallel, the ABA-independent pathway also activates MYB/WRKY genes, which are also activated by the Ca signal and also the ROS signal stimulated by the cold signal. Both ABA-dependent and ABA-independent genes get activated and took part in cold acclimatization and freezing tolerance. *SA* salicylic acid, *ABA* abscisic acid, *ROS* reactive oxygen species, *bZIP* basic region-leucine zipper type transcription factors, *LEA* late embryonic abundant proteins, *ABRE* ABA-responsive element, *RVE4 and 8* Protein REVIELLE4 and 8, *CBF* C-repeat binding factor, *AP21* ??, *ERF1* ethylene-responsive factor1, *MYB* MYB transcription factor, *WRKY* WRKY transcription factor, *COR* cold responsive

temperature induced, and cold inducible, encoding protective proteins like osmolytes and cryoprotectants to safeguard plants from freezing injuries (Yamaguchi-Shinozaki and Shinozaki 2006).

CBF1–3 (*CBF1/DREB1B*, *CBF2/DREB1C*, and *CBF3/DREB1A*), are the three *Arabidopsis CBF* genes organized in repeated sequence on chromosome IV (Medina et al. 1999). Freezing stress tolerance is enhanced in overexpressed *DREB1A*, transgenic *Arabidopsis. Arabidopsis*, rice, and soybeans exhibit cold-inducible *ABRE*-dependent gene expression (Maruyama et al. 2012). Another *CBF* gene in *Arabidopsis*, *CBF4*, is not cold-induced, yet its overexpression augments to withstand freezing and drought in plants (Haake et al. 2002). These *CBF* genes, categorized as *AP2/ERF1*-type transcription factors, specifically attached to conserved

CRT/DRE motifs in COR gene promoters (*CBF* regulons), and express under cold conditions (Maruyama et al. 2012).

Murayama et al. (2004) also identified the downstream gene that *DREB1A* regulates and divided the genes into two categories. While one group deals with drought, freezing stress, and high salt, another group has antifreezing and LEA protein functions. According to Wang et al. (2022), rice *OsDREB1C*, *OsDREB1E*, and *OsDREB1G* mutants were able to acclimate to cold, suggesting that these rice *DREB1* genes are crucial for basal chilling tolerance but not for cold acclimation. Overexpression of transgenic rice *OsDREB1A or DREB1A* accumulates different sugars and osmoprotectants like proline (Ito et al. 2006). *OsDREB1A* targets genes that may be involved in chilling stress tolerance, such as dehydrin genes. The existence of the low-temperature responsive (LTR) element within the promoter of *PnaDREBs* highlights its significance in responding to CS (Qian et al. 2023). Overexpression of *DREB1/CBF* genes from different kinds of plants, including rice, tomato, and barley, significantly enhances cold tolerance, suggesting evolutionary conservation in higher plants. *MaDREB1F* overexpression in bananas increases resistance to drought and CS by activating protective metabolites, antioxidant systems, and jasmonate and ethylene syntheses (Xu et al. 2023)

Additionally, the overexpression of transcription factors like *BpERF13* enhances cold tolerance in woody plants like birch, apple, and radish, thereby modulating osmotic adjustment and cell wall mechanical strength (Lv et al. 2020).

For a comprehensive overview of *CBF/DREB1*-dependent COR gene expression in various plant species, refer to Table 9.1.

9.3.2 Role of MYB Genes in Conferring Plant Cold Tolerance

The MYB domain consists of 1–4 repetitive sequences (R) containing 50–52 amino acids have a highly conserved region in the DNA-binding called as MYB transcription factor family. Based on the sequences MYB transcription factors are categorize into four separate subfamilies: *R1-MYB/MYB*, *R2R3-MYB*, *R1R2R3-MYB*, and *4R-MYB*. Among these, the extensively studied subfamily is the *R2R3-typ*e MYB (Yang et al. 2022). In the context of plant cold tolerance, investigations into the regulatory mechanisms of *R2R3-MYBs* have primarily focused on apple and pear. For instance, in apple overexpression of *MdMYB308L* significantly heightened cold tolerance (An et al. 2020). Similarly, in pear, expression *of PbrMYB5* was triggered under CS, and its overexpression enhancing the cold resistivity was study in transgenic tobacco (Xing et al. 2019).

Notably, a few R2R3-MYB transcription factors, such as HOS10 in *Arabidopsis* and Osmyb4 in rice, have been suggested to play pivotal roles in CS responses (Dai et al. 2007). Additionally, in chrysanthemum overexpressing *DgMYB2,* a cold-induced R1-MYB transcription factor, increased cold resistance. DgMYB2 directly act on *DgGPX1* to boosting activity of GPX enzyme, subsequently it reduces accumulation of ROS and bolstering chrysanthemum's cold resistance (Yang et al.

Table 9.1 Signalling components dependent on CBF/DREB conferring plant cold tolerance

Sl. no.	Name of the gene	Source plant	Effect on plants	References
1.	*AtCBF1*	*Arabidopsis thaliana*	Freezing, salt and drought tolerance	Jaglo-Ottosen et al. (1998)
2.	*AtCBF3*	*Arabidopsis thaliana*	Freezing, salt and drought tolerance	Gilmour et al. (1998)
3.	*ZmDREB1A*	*Zea mays*	Salt, drought and freezing tolerance	Feng et al. (2004)
4.	*OsDREB1A* *OsDREB1B* *OsDREB1C*	*Oryza sativa*	Salt, drought and chilling tolerance	Ito et al. (2006)
5.	*HvCBF4*	*Hordeum vulgare*	Salt, drought and chilling tolerance	Oh et al. (2007)
6.	*BpCBF1*	*Betula pendula*	Freezing tolerance	Welling and Palva (2008)
7.	*LpCBF3*	*Lolium perenne*	Freezing tolerance	Zhao and Bughrara (2008)
8.	*GmDREB3*	*Glycine max*	Drought, salt and freezing tolerance	Chen et al. (2009)
9.	*TaDREB2* *TaDREB3*	*Triticum aestivum*	Drought and frost tolerance	Morran et al. (2011)
10.	*MbDREB1*	*Malus baccata*	Chilling, drought and salt tolerance	Yang et al. (2011)
11.	*PbeNAC1*	*Pyrus betulifolia*	Drought and cold tolerance	Jin et al. (2017)
12.	*SlCBF1*	*Solanum lycopersicum*	Chilling tolerance	Li et al. (2018)
13.	*BpERF13*	*Betula platyphylla*	Cold tolerance	Lv et al. (2020)
14.	*OsSAPK6*	*Oryza sativa*	Chilling tolerance	Jia et al. (2022)
15.	*MbCBF2*	*Malus baccata*	Cold and salt tolerance	Li et al. (2022)
16.	*MbCBF1*	*Malus baccata*	Salt and cold tolerance	Liang et al. (2022)
17.	*LmTrxh2*	*Lobularia maritima*	Cold tolerance	Ben Saad et al. (2023)
18.	*RsERF40*	*Raphanus sativus*	Cold tolerance	Li et al. (2023a, b)
19.	*MaDREB1F*	*Musa accuminata*	Cold and drought tolerance	Xu et al. (2023)

2022). Moreover, in cold sensitive rice, cold-inducible R1R2R3 MYB TF, *OsMYB3R-2*, has been reported. This factor exhibited increased expression after cold treatment and demonstrated accumulation over 72 h. Unlike Osmyb4, which responds solely to CS, *OsMYB3R-2* was discovered to be caused by drought and salt stress as well (Dai et al. 2007). For a comprehensive overview of MYB genes associated with conferring cold tolerance among different plant species, refer to Table 9.2.

Table 9.2 MYB genes conferring plant cold tolerance

Sl no.	Name of the gene	Source plant	Effect on plants	References
1.	*Osmyb4*	*Oryza sativa*	Increased freezing and chilling tolerance	Vannini et al. (2007)
2.	*OsMYB3R-2*	*Oryza sativa*	Enhanced tolerance towards drought, freezing, and salt stress	Dai et al. (2007)
3.	*OsMYB3R-2*	*Oryza sativa*	Resistance to cold stress	Ma et al. (2009)
4.	*OsMYBS3*	*Oryza sativa*	Enhanced cold tolerance	Su et al. (2010)
5.	*TaMYB2A*	*Triticum aestivum*	Enhanced tolerance towards drought, salt, and freezing stress	Mao et al. (2011)
6.	*MdoMYB121*	*Malus domestica*	salinity, drought, and cold stresses	Cao et al. (2013)
7.	*GmMYBJ1*	*Glycine max*	Enhanced cold and drought tolerance	Su et al. (2014)
8.	*MdMYB4*	*Malus domestica*	Increased cold and salt stress	Wu et al. (2017)
9.	*MdMYB23*	*Malus domestica*	Enhanced cold tolerance	An et al. (2018)
10.	*MbMYB4*	*Malus baccata*	Drought and cold tolerance	Yao et al. (2022)
11.	*DgMYB2*	*Dendranthema grandiflora*	Cold tolerance	Yang et al. (2022)

9.3.3 Role of WRKY *Genes in Cold Tolerance*

In plants the WRKY transcription factor (TF) family, is considered to be largest, primarily occurs in higher plants, but rarely found in lower plants. It plays diverse roles in various biological processes. These genes have the potential to enhance an individual's ability to survive in CS conditions by raising antioxidant activity levels, preserving membrane stability, and improving osmotic regulation ability (Bakshi and Oelmuller 2014; Khoso et al. 2022). The WRKY or Sweet Potato Factor 1 (SPF1) gene was first studied from sweet potatoes (Ishiguro and Nakamura 1994). Subsequence studies has identified and characterized WRKY from a variety of plants, which including 72 WRKY TFs in *Arabidopsis thaliana* and 103 WRKY members in *Oryza sativa* (Eulgem and Somssich 2007; Ramamoorthy et al. 2008). These TFs share a highly conserved DNA-binding domain of approximately 60 amino acids known as the WRKY domain. This domain comprises the conserved WRKYGQK sequence at the N-terminal and a zinc-finger structure at the C-termina (Jiang et al. 2017).

Although the core DNA binding motif of WRKY proteins is mostly WRKYGQK, variations such as WKKYGQK, WRKYGMK, WSKYGQK, WKRYGQK, WVKYGQK, and WRKYGKK have been observed (Huang et al.

2012; Xie et al. 2005). These differences in the WRKY domain, along with the structural features of zinc-finger motifs, categorize WRKY proteins into three groups: I, II, and III. Group I WRKY proteins has two WRKY domains and a C2H2 zinc-finger structure, while Group II comprises WRKY proteins with one WRKY domain and a C2H2 zinc-finger structure. Group III consists of WRKY proteins having only single WRKY domain and a C2HC-type zinc finger (Wu et al. 2005). The WRKY34 (WRKY group I) TF might take part in the C-repeat binding factor (CBF) signal cascade in mature pollen and mature *Arabidopsis* pollen it negatively regulated the cold sensitivity (Zou et al. 2010). SlWRKY50, a Group II WRKY transcription factor that is cold inducible, reacts to cold stimuli, and is essential for the biosynthesis of JA, according to research by Wang et al. (2023). The tomato *allene oxide synthase* gene (*SlAOS*) promoter is directly bound by *SlWRKY50*, and overexpressing *SlWRKY50* increased tomato resistance to chilling.

WRKY genes have been found to be identified to orchestrate multiple biological processes. For example, *AtWRKY33* regulates disease resistance, NaCl tolerance (Birkenbihl et al. 2012), and thermotolerance, while *CaWRKY40* in pepper modulates resistance to *Ralstonia solanacearum* and heat stress tolerance (Dang et al. 2019). Specifically, in rice plants, *OsWRKY71* responds specifically to cold stress, targeting potential downstream genes *OsTGFR* and *WSI76* upon cold treatment. Overexpression of *OsWRKY71* enhances cold tolerance in transgenic rice, validated by assessments such as chlorophyll fluorescence (Liu et al. 2007). Expression of *GhWRKY41* was observed significantly at 4 °C. After the cotton was exposed to cold treatment, the level of *GhWRKY15* expression was also elevated (Guo et al. 2022). *V. bonariensis* demonstrated a higher induction of *VbWRKY32* overexpression (OE) in leaves compared to wild-type (WT), which increased the plant's resistance to cold. The results showed that *VbWRKY32* functioned as a positive regulator by upregulating the levels of gene transcription that responded to cold (Wang et al. 2020a, b). In white clover under cold stress, *TrWRKY* genes were sharply up-regulated; specifically, at 30 min, 43 *TrWRKY* genes were up-regulated, suggesting that these *TrWRKY* genes responded to cold stress rapidly (Li et al. 2023a, b).

Research has demonstrated the induction of WRKY gene expression under both cold and salt stresses in plants. Investigating the role of *KoWRKY40* in cold stress response, transgenic *Arabidopsis* plants overexpressing KoWRKY40 were developed. Under CS, *KoWRKY40* expression was notably heightened in the roots and leaves of *K. obovate* (Fei et al. 2022). Table 9.3 summarizes WRKY genes associated with conferring cold tolerance in various plant species.

Table 9.3 WRKY genes conferring plant cold tolerance

Sl no.	Name of the gene	Source plant	Phenotype and effect	References
1.	*GmWRKY21*	*Glycine max*	Freezing tolerance	Zhou et al. (2008)
2.	*TaWRKY19*	*Triticum aestivum*	Tolerance to freezing, salt and drought stress	
3.	*BcWRKY46*	*Verbena bonariensis*	Increased tolerance towards cold, salt and dehydration	Wang et al. (2012)
4.	*OsWRKY76*	*Oryza sativa*	Cold tolerance	Yokotani et al. (2013)
5.	*OsWRKY74*	*Oryza sativa*	Cold tolerance	Dai et al. (2016)
6.	OsWRKY71	*Oryza sativa*	Cold tolerance	Kim et al. (2016)
7.	*CsWRKY46*	*Cucumis sativus*	Highly sensitivity to ABA; Freezing tolerance	Zhang et al. (2016)
8.	*VbWRKY32*	*Verbena bonariensis*	Increased cold tolerance	Wang et al. (2020a)
9.	KoWRKY40	*Kandelia obovata*	Cold tolerance	Fei et al. (2022)

9.4 Genetic and Epigenetic Factors Contributing to the Diversification of Cold Stress Response

Since plant lack a brain to retain memories, it senses and reacts to heat and CS, which is controlled by epigenetic modifications and have an important function in gene regulation. The ability to develop suitable molecular and physiological changes results from this. Furthermore, stress memories that are epigenetically regulated are passed down to subsequent generation (Ramakrishnan et al. 2022). Salicylic acid is essential for the activation of the salicylic acid responsive gene, and downstream signalling proteins influence both the memory process and alteration of the chromatin for these target genes. High levels of H3 acetylation, H4 acetylation, and H3K4 methylation brought on by salicylic acid (Bhadouriya et al. 2021). Modifications of Flowering Locus C (FLC) gene's to H3K27me3 preserve CS memory. This shows that accessibility of chromatin and structure, which are frequently linked to epigenetic codes or epigenetic regulations like DNA methylation, histone variants, and posttranslational modifications (PTMs), are crucial for controlling the expression of genes(Xie et al. 2023).

9.4.1 Histone Modification

Plant acclimation to cold conditions gradually diminishes after vernalization, representing a prominent instance of plant epigenetic regulation in reaction to environmental cues (Kang et al. 2022). Genetic and molecular investigations have demonstrated the pivotal part of epigenetic markers in vernalization, where an epigenetic memory governs the plant's response (Sharma et al. 2022). Research has demonstrated that changes to histones, including methylation and acetylation, undergo alterations during CS, impacting various molecular mechanisms, especially genes that respond to cold and can be genetically altered (Bhadouriya et al. 2021).

Post-translational modifications (PTMs) of histones entail the chemical modification of specific amino acid residues—lysine, arginine serine and threonine—in the histone tail. These PTMs have capacity to modulate chromatin dynamics and structure, consequently impacting the way that stress-responsive genes are expressed by recruiting histone modifiers (Ramakrishnan et al. 2022). Chromatin conformation plays a crucial part in determining the accessibility of DNA sequences, including regulatory and coding parts, to the transcriptional apparatus, thereby governing gene expression. Nucleosome positioning mediates DNA accessibility for transcription, with each core nucleosome comprising H2A, H2B, H3, and H4 histone proteins and roughly 146 DNA base pairs (Mariño-Ramírez et al. 2005).

In plants during CS histone modifications and DNA methylation are prominent epigenetic markers. During acetylation an acetyl group is transfer to lysine residues of the histone tail, performed by histone acetyltransferases (HATs). This modification leads to an "open" chromatin configuration, facilitating transcriptional activation. On exposure to abiotic stress in plants, stress-related genes are activated by the interaction between HATs and transcription factors (Pandey et al. 2002). Through chromatin configuration, genes expression is silence through histone deacetylation which regulated by histone deacetylases (HDACs). Histone methylation, conducted by histone methyltransferases (HMTs), also plays a significant role. In potato, genomic regions housing active regulatory elements, recognized as DNase I hypersensitive sites (DHSs) via chromatin analysis, exercise significant regulatory authority over cold stress response (Zeng et al. 2019).

Specific histone modifications including H3K4me3 and H3K27me3 act as memory marks for stress-responsive genes of *Arabidopsis* (Kwon et al. 2009). CS promotes these modifications and improve chromatin accessibility, making it easier for regulatory proteins needed for up or down-regulation of genes (Zeng et al. 2019). Histone acetylation typically facilitates gene expression. Histone H3 acetylation stimulates COR gene activation during cold stress, with the HAC1 histone acetyltransferase being essential for stress memory and augmenting cold memory (Roy et al. 2014). Conversely, cold exposure triggers histone deacetylation through the increased control of histone deacetylases (HDACs), resulting in deacetylation of histone subunits H3 and H4, which represses genes sensitive to cold expression such as *ZmDREB1* and *ZmCOR413* in Zea mays (Hu et al. 2011). The gene product of

HOS15, operating as a histone deacetylation factor, specifically interacts with histone H4 during cold acclimatization in *Arabidopsis* (Park et al. 2018).

9.4.2 DNA Methylation

DNA methylation, involving in addition of methyl group to cytosine at CpG sites, orchestrates DNA stability, chromatin architecture, and gene expression without altering in its DNA sequence. In plant genomes, it spans heterochromatic and euchromatic regions, encompassing gene promoters, intergenic spaces, transposable elements (TEs), and gene bodies (Zilberman and Henikoff 2007). Studies highlight 5-methylcytosine (5mC) and N6-methyladenine (6 mA) as regulators of transcription during cold stress responses (Zhang et al. 2018), moreover, cold-induced DNA methylation changes can be passed across generations or as epigenetic memories for subsequent cold stress responses in plants (Verma et al. 2022). DNA methylation as well as demethylation, induces during cold acclimation, impacting freezing tolerance in *Arabidopsis* and RNA-directed DNA methylation (RdDM) in cucumbers. Vernalization-triggered demethylation varies among plants, influencing non-CG methylation via mitosis (Liu and He 2020). DNA methylation contributes to transposable element (TE) silencing and environmentally driven alterations in the DNA methylome may promote or suppress TE activity. While DNA methylation in *Arabidopsis* is minimally influenced by temperature and other stresses, it exhibits weak environmental sensitivity, potentially not inducing extensive gene expression changes within a single generation (Ganguly 2018).

9.4.3 Non-coding RNAs

Non-coding RNAs (ncRNAs) are essential for many characteristics of plant biology, such as growth, development, and response to diverse environmental stressors (Bhogireddy et al. 2021) These ncRNAs are categorized based on its nucleotides length. ncRNA with 20–200 nucleotides are small and above 200 nucleotides are considered as long. Trans-acting small interfering RNAs (ta-siRNAs), micro-RNAs (miRNAs), heterochromatic (hc-RNAs), and small natural-antisense siRNAs (na-tsiRNAs) are few of the small ncRNAs in plants. The significance of long non-coding RNAs (lncRNAs) has been highlighted bi-genome-scale surveys in plants in regulating responses to CS. For example, in cassava, biosynthesis of hormone signaling, sucrose metabolism, and secondary metabolite biosynthesis were associated 318 lncRNAs, indicating their part in CS tolerance (Li et al. 2017). Similarly, studies in grapevine identified 284 lncRNAs lncRNAs that respond to cold, alongside genes coding for 326 proteins (Wang et al. 2019).

Furthermore, Under CS conditions certain lncRNAs act as goal imitators for miRNAs. For instance, LincRNA159 functions as a goal imitator for miR164 in cassava, which lowers the expression of NAC genes (Li et al. 2017). In *Brassica napus*, a recent study by Waseem et al. (2022) investigated the expression alterations of lncRNAs in cold-sensitive and cold-tolerant varieties under CS. They identified 11,073 lncRNAs, of which 4819 were expressed differently in response to CS. Interestingly, in silico investigation identified 16 lncRNAs acting as predecessors of seven B. napus particular miRNA families and 15 lncRNAs expected to be targets of 23 miRNAs. Numerous miRNAs have been recognized as important participants in the way plants react to CS. In rice, downregulation of Osa-miR319b due to CS leads to the downregulation of *OsPCF6* and *OsTCP21*, which in turn upregulate cold stress-responsive genes like *DREB1/CBF*, *DREB2A*, and *TPP1/2*, ultimately enhancing CS tolerance (Wang et al. 2014) Additionally, in *Arabidopsis*, several hundred lncRNAs were differentially expressed under various abiotic stresses, while 813 lncRNAs in grapevine, under CS (Wang et al. 2019).

9.4.4 Circular RNAs

Circular RNAs (circRNAs) describe a distinct class of endogenous non-coding RNAs define by its unique closed-loop arrangement. These circular transcripts are predominantly derived from genes coding proteins and can comprise of either only exons or multiple exons (Santer et al. 2019). circRNAs lack conventional 5′ caps and poly(A) tails, yet it is generated inside the nucleus, typically transported to cytoplasm (Salzman et al. 2012). Plants under CS response has a distinct expression of circRNAs. For instance, analyses in chilled bell pepper and chilled tomato fruit identified 36 and 163 differentially expressed circRNAs, respectively (Zuo et al. 2016). Similarly, 475 differently expressed circRNAs were found in grape leaves after it was exposed to CS (Gao et al. 2019). Zhang et al. (2020) elucidated the mechanism by which Vv-circATS1 operates. It was found that this circRNA regulates the expression of various stress-responsive genes, including *CSD2*, *PRXCA*, *PME41*, *LOX3*, and *WRKY48*, thereby improving cold tolerance in *Arabidopsis*. The identified grapevine circRNA, Vv-circATS1, originating from glycerol-3-P acyltransferase, exhibits a potential role in enhancing CS resilience in plants by regulating the genes expression which is crucial in responding to environmental stimuli, as evidenced in *Arabidopsis* (Gao et al. 2019)

9.5 Comparative Analysis Between Arabidopsis and Rice During Cold Stress Response

The DREB1-type ERF/AP2 proteins in monocots share a close phylogenetic relationship, in compare to their dicot counterparts. Noteworthy is the binding affinity difference exhibited by the *Arabidopsis* AtDREB1A and rice OsDREB1A proteins.

AtDREB1A binds ACCGAC and GCCGAC equally, while OsDREB1A prefers GCCGAC over ACCGAC (Dubouzet et al. 2003). In rice It is clear the *DREB1/CBF* cold-responsive pathway is conserved. In transgenic *Arabidopsis* excessive expression of *DREB1* or *OsDREB1* induces robust expression of stress-responsive genes, enhancing high-salt and freezing stresses tolerance. Transgenic rice with upregulated *OsDREB1* or *DREB1* levels exhibit lower growth under natural conditions but enhanced resilience to drought, low-temperature and high-salt (Ito et al. 2006).

The CBF/DREB1 family, comprising six genes in *Arabidopsis* and ten in rice (*OsDREB1A* to *OsDREB1J*), shows distinct responses to CS. *OsDREB1A*, *OsDREB1B*, and *OsDREB1F* are induced, while *OsDREB1D* remains unaffected. Overexpression of *OsDREB1A*, *OsDREB1D*, and *OsDREB1F* enhances cold resistance in *Arabidopsis* through elevated COR expression (Mao and Chen 2012). Rice, under cold stress, sequentially upregulates *OsDREB1B*, *OsHsfA3*, and trehalose-6-phosphate phosphatase, contributing to cold acclimation *via* trehalose synthesis. In *Arabidopsis*, *ATGOLS3* and *BBX14* are upregulated during CS (Nakamura et al. 2011).

Distinct cold-inducible promoter sequences are identified in *Arabidopsis* and rice (Maruyama et al. 2012). ACACGT and AATATC are the most conserved sequences in *Arabidopsis*, while CGTACG and GTAGTA are most conserved in rice. Promoter analyses reveal the absence of highly conserved motifs akin to DRE or ABRE in rice promoters. 22 genes *OsDREB1c* regulon was identified by Zhang et al. (2012) with 18 differentially expressed in cold-stressed *japonica* rice (cv. Jumli Marshi), highlighting the crucial part of the *OsDREB1c* regulon in cold tolerance. Comparative transcription profiles under CS highlight similarities between rice and *Arabidopsis*. Both species exhibit upregulation of dehydrin and Late Embryogenesis Abundant Protein genes (*LEA*) and genes relating downregulation of photosynthesis activity. In the promoters of cold-inducible *Arabidopsis* and the DREB1A regulated downstream genes have highly conserved DRE motif. This comparison underscores the conservation and divergence within plants in cold-responsive pathways between monocots and dicots, providing insights into the intricate molecular process controlling stress responses (Mikołajczak et al. 2023).

Gene expressional examination profiles in *Arabidopsis* indicated a noteworthy representation of the transcription factors from the AP2/ERF family. In action against low temperatures rice deploys three principal signal cascades: the DREB1/CBF pathway, a MAPK cascade, and an ABA-dependent pathway. This intricate network involves the activation of various genes, such as calcium-dependent protein kinases (*CDPKs*), including *OsCDPK4*, *OsCDPK5*, and OsCDPK7, as well as a cytochrome P450 monooxygenase gene, *CYP76M8,* and a peroxidase gene, *POX-1*, during chilling exposure. Concomitantly, OsMYB3R-2 and OsMYB2 have been identified as contributors to enhanced tolerance to low temperatures. Notably, the upregulation of a heat shock protein analogous to HSP70B (Os01g0688900) is observed early in the chilling stress response (Buti et al. 2019).

The role of lipid transfer proteins (LTPs) in freezing tolerance is highlighted by the overexpression of LTP3 in *Arabidopsis*. In rice, specific LTPs, including LTP7, LTP8, LTP12, and LTP25, demonstrate an early and maximal activation following

3 h of cold exposure, particularly in the cold-tolerant cultivar *Nipponbare* (Moraes de Freitas et al. 2019). Cyclic nucleotide-gated channels (CNGCs), functioning as general cation channels, has a critical role in different type of stress responses, such as low temperatures, in *Arabidopsis*. However, in rice, the chilling tolerance divergence is connected to *CHILLING-TOLERANCE DIVERGENCE 1 (COLD1)*. In rice G-protein a subunit 1 (RGA1) and G-protein signalling (RGS), regulatory effects of COLD1 by increasing GTPase activity, is similar to *AtRGS1*. Although COLD1's subcellular localization pattern partially overlaps with its *Arabidopsis* orthologs GTG1/2, distinctions exist, especially in intrinsic GTPase activity (Wei et al. 2021).

In absence of a low-temperature stimulus it was found transgenic *Arabidopsis* plants overexpressed *SCOF-1* and exhibit constitutive expression of *Cold Response (COR)* genes, such as *COR15a*, *Rd29B*, and *COR47*. This overexpression enhances cold tolerance in non-acclimated transgenic plants. In the context of dehydration and ABA response pathways, the bHLH protein rd22BP1 is identified in *Arabidopsis*. A comparative analysis with its rice counterpart, *OsbHLH1*, reveals divergence in identity (25%) and amino acid conservation, suggesting different target elements. *OsbHLH1* likely to be ABA-independent cold-induce, highly expressed in roots while it's expression patterns is also different. In contrast, *rd22BP1* is highly expressed in siliques and stems induce mainly by dehydration, in ABA-dependent manner, but not in leaves and roots. These indicates that *OsbHLH1* and *rd22BP1* participate distinctly in abiotic stress responses, by means of ABA-independent and ABA-dependent signal-transduction pathways (Yang et al. 2023).

9.6 Conclusions

The distribution of plants across latitudes and altitudes is influenced by low temperatures, however, less than half of the plant families belonging to the angiosperm are able to withstand seasonal low temperatures. Forecasts predict an increased global temperature rise around 1.1–6.4 °C in the next 80 years, potentially increasing the constancy and rigidity of warm winter spells. Traits induced by cold conditions, like cold acclimation, endodormancy, and vernalization responsiveness, have developed autonomously several times in angiosperms, modifying shared genetic pathways. Many key regulators of these traits belong to sizable gene families involved in stress responses and developmental transitions.

The understanding of CS response in plants has significantly progressed over the years, delving into intricate molecular mechanisms, signalling pathways, and genetic regulation. Abiotic stressors, especially those related to cold, pose substantial challenges to plant growth, development, and productivity. Plants exhibit diverse adaptive strategies, mechanisms, and genetic pathways to deal with low-temperature stress. Knowing the molecular processes that underlie plant reactions to cold stress is essential for the advancement of resilient crop varieties with improved cold tolerance. Advances in molecular tools, genome editing techniques, and biotechnological approaches have provided avenues for the manipulation and enhancement of cold stress tolerance in crops.

Recent research on circRNA identification in plants highlights a potential area for knowing their respective functions in growth and development of the plant, biotic and abiotic stress responses, akin to their roles in animals' gene expression regulation. Pathways like the *CBF/DREB1*-dependent pathway perform a central function in controlling cold signalling, involving factors such as Ca^{2+} signalling, chloroplast status, clock genes, and phytohormones. Phytohormone induced metabolic pathway manipulation via genetic engineering mechanism growth patterns can be modified to withstand cold stress.

Given the threat of biotic and abiotic stresses to agriculture-based economies and food security, understanding CS adaptation at the genomics and proteomics stage can identify genes and proteins associated with cold tolerance. Environmental changes necessitate plants to adapt growth physiology against various stresses. Extensive research on epigenetic marks (DNA methylation, histone modifications, diverse RNA forms, ATP-mediated regulations) aims to modulate the accessibility of stress-responsive genes. Sophisticated sequencing technologies and chromatin profiling have propelled epigenetic studies, especially in crop plants, addressing food security challenges.

The exploration of transcription factors like CBF/DREB1, and MYB and WRKY genes has shed light on their pivotal roles in conferring cold tolerance in various plant species. The *CBF/DREB1* pathway, in particular, emerges as a key regulator, inducing the genes sensitive to cold expression and enhancing freezing tolerance. Additionally, MYB and WRKY transcription factors play critical function in modulating plant responses to CS, contributing to the activation of protective methods.

Moreover, the study of non-coding RNAs, specifically circular RNAs (circRNAs), has drawn notice for their involvement in plant stress responses, including cold stress. Differentially expressed circRNAs, such as Vv-circATS1 originating from glycerol-3-P acyltransferase in grapevines, have shown the ability to withstand cold in Arabidopsis by regulating the stress-responsive genes expression. DNA methylation and histone modification are examples of epigenetic modifications showing crucial for supporting plants to adapt in CS. These changes affect the expression of genes and the structure of chromatin, which helps the plant tolerate low temperatures.

This comprehensive review highlights the diverse molecular pathways, signalling molecules, hormonal dynamics, epigenetic modifications, and genetic elements that is responsible in plant CS. Future research in this field should continue to explore novel genetic targets, regulatory networks, and signalling pathways to further elucidate and enhance our knowledge on how plants respond and adapt to CS, ultimately opening the door for the creation of crop varieties resistant to stress, which are essential for maintaining global food security in the face of shifting environmental conditions.

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