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REVIEW ARTICLE

AP2/ERF, an important cold stress-related transcription factor family in plants: A review

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Abstract Increasing the vulnerability of plants especially crops to a wide range of cold stress reduces plant growth, development, yield production, and plant distribution. Cold stress induces physiological, morphological, biochemical, phenotypic, and molecular changes in plants. Transcription factor (TF) is one of the most important regulators that mediate gene expression. TF is activated by the signal transduction pathway, together with *cis*-acting element modulate the transcription of cold-responsive genes which contribute to increasing cold tolerance in plants. Here, AP2/ERF TF family is one of the most important cold stress-related TF families that along with other TF families, such as WRKY, bHLH, bZIP, MYB, NAC, and C2H2 interrelate to enhance cold stress tolerance. Over the past decade, significant progress has been found to solve the role of transcription factors (TFs) in improving cold tolerance in plants, such as omics analysis. Furthermore, numerous studies have identified and characterized the complexity of cold stress mechanisms among TFs or between TFs and other factors (endogenous and exogenous) including phytohormones, eugenol, and light. The role, function, and relationship among these TFs or between TFs and other factors to enhance cold tolerance still need to be clarified. Here, the current study analysed the role of AP2/ERF TF and the linkages among AP2/ERF with MYB, WRKY, bZIP, bHLH, C2H2, or NAC against cold stress tolerance.

Keywords Abiotic stress · Cold stress · Cold tolerance · Low temperature · Transcription factors

Abbreviations

CA	Cold acclimation
TF	Transcription factor
TFs	Transcription factors
ABA	Abscisic acid
JA	Jasmonic acid
SA	Salicylic acid
CAMP	Cyclic adenosine monophosphate
ROS	Reactive oxygen species
CBL	Calcineurin-B Like proteins
CPKs/ CDPKs	Ca^{2+}-dependent protein kinases
CIPKs	CBL-interacting protein kinases
CBF	C-repeat Binding Factor
DREB	Dehydration-Responsive Element-Binding-Factor
ICE1	CBF expression 1
COR	Cold regulated genes
AP2/ERF	APETALA2/Ethylene responsive factor
DRE/CRT	Dehydration-responsive C-repeat
ChIP-seq	Chromatin Immunoprecipitation-sequencing
ChIP-PCR	Chromatin Immunoprecipitation Polymerase Chain Reaction
SOD	Superoxide
POD	Peroxide

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CAT	Catalase
APX	Ascorbate peroxidase
BIN2	Brassinosteroid-Insensitive2
HOS1	Osmotically Responsive Gene1
GA	Gibberellic Acid
phyA	Phytochrome A
phyB	Phytochrome B
PIFs	Phytochrome-Interacting Factors
bHLH	Basic helix-loop-helix
LEA	Late embryogenesis abundant
bZIP	Basic leucine zipper
MYB	Myeloblastosis

Introduction

Global warming drives a drastic change in climate, which is accompanied by an increase in intensity and frequency of abiotic stresses including temperature, salinity, and drought stress (Watt et al. 2020; Zandalinas et al. 2021). Meanwhile, plants are sessile and acclimatize to these abiotic stresses (Beloiu et al. 2020). Cold stress (0–15 °C) and freezing stress (< 0 °C) are the major stresses in temperate and few subtropical areas that adversely influence plant growth and development, reduce yield production (Kang et al. 2020; Ritonga et al. 2021), and also cause worldwide economic losses in crop production. Cold stress generally alters all physio-chemical pathways of a living cell that influences enzyme activity, solute diffusion rates, membrane fluidity, and reverse the interactions of macromolecules like DNA, RNA, and proteins (Gualerzi et al. 2003).

Cell membrane and cell structure stability is the key point for plants survival under cold stress (Chen et al. 2018). Freezing stress leads to ice formation in plant tissues (Puhakainen et al. 2004). This phenomenon causes into the extracellular space of plant cells filled with ice crystals which leads to dehydration due to the water flowing (Ritonga and Chen 2020). Moreover, cold stress alters metabolic pathways of anthers to induce pollen sterility (Sharma and Nayyar 2016). Cold stress induces ovule infertility, flower abortion, fertilization breakdown and low quality of seed, and eventually lead to low grain yield in plants (Thakur et al. 2010; Alisoltani et al. 2019). Cold/freezing stress also leads to withered, dwarfism, and chlorosis in plants (Yadav 2010; Gu et al. 2019).

The ability of plants to survive under cold stress is referred to cold acclimation (CA) process (Kargiotidou et al. 2010). It was shown that non acclimated *Arabidopsis thaliana* is more sensitive to freezing stress (-20 °C) compared to 4 °C cold-acclimated *A. thaliana* under (Yu et al. 2021). The severity of the cold stress effect is related to species genotype, stress intensity, and the duration of cold exposure (Carvallo et al. 2011; Londo et al. 2018; Mehrotra et al. 2020). Prerostova et al. (2021) found that hormones such as salicylic acid (SA), jasmonic acid (JA), and abscisic acid (ABA) were elevated in the crowns, leaves, and plant roots under cold stress. Besides, antioxidant enzyme activities protect plants from higher H_2O_2 and O_2^- content under cold stress (Zhao et al. 2021). Over the past ten years (2010–2020), numerous studies had revealed that transcription factors (TFs) are primary regulators associated with cold stress (Mitsis et al. 2020). TFs play vital roles in regulating signal transduction, as well as gene expression under cold stress (Chen et al. 2015a). Several cold stress-responsive TF families have been analyzed and identified in numerous plant species (Mehrotra et al. 2020), including AP2/ERF (Byun et al. 2015; Lv et al. 2019), NAC (Nakashima et al. 2012), WRKY (Zhang et al. 2016), bZIP (Liu et al. 2018a), bHLH (Yao et al. 2018), and MYB (Su et al. 2014). Interestingly, TFs and stress-responsive genes regulate the plant's responses during and after cold/freezing stress (Mizoi et al. 2012).

Kashyap and Deswal (2017) reported the expression of C-repeat binding factor (CBF) gene from *Hippophae rhamnoides* (*HrCBF*) initially increased after 0.5 h of 4 °C exposure and continue to increase at 1 h, 3 h, 6 h, 24 h, and 1 week of cold exposure. Overexpression of *CBF1* of *Prunus persica* (*PpCBF*) in *Malus domestica* was observed for three years in three growing seasons. It was revealed that *PpCBF1* regulated anthocyanine and carotenoid content of transgenic apple during fall seasons, while *PpCBF1* regulated plant height and lateral branches of transgenic apple during summer. These results illustrated that *PpCBF1* functions during and after cold stress in transgenic *M. domestica* (Artlip et al. 2014). Some TFs also interact with other TFs to activate or repress the general transcriptional process (Eulgem and Somssich 2007). The current study summarized the role of AP2/ERF TF and the understanding of different TFs involved in cold stress to develop plant species resistant to low temperatures to achieve agricultural and forestry sustainability through TFs utilization.

Cold stress tolerance mechanism in plants

Plants utilize structural modifications such as alteration of membrane fluidity, protein structure transformation, and cytoskeleton movement, to respond and adapt to cold stress (Mehrotra et al. 2020). Previous studies have revealed that plants have different sensory levels under cold stress (Luo et al. 2020a). However, cold stress is initially sensed by receptors on plant membrane, which alter membrane fluidity and subsequently induce calcium cation (Ca^{2+}), cyclic adenosine monophosphate (CAMP), and reactive oxygen species (ROS) production. Chloroplast also acts as a signal modulator to the nucleus through ROS production. Ca^{2+} signaling acts as a mediator of plant response to cold stress (Yuan et al. 2018). Meanwhile, Ca^{2+}, CAMP, and ROS signaling mediate signal transduction via Calcineurin-B Like proteins (CBL), Ca^{2+}-dependent protein kinases (CPKs/CDPKs) and CBL-interacting protein kinases (CIPKs) to the nucleus via a pathway interceded by ICE-CBF/DREB TFs.

In general, cold stress mechanism in plants involves the inducer of CBF expression 1 (ICE1), an inducer of CBF/Dehydration-Responsive Element-Binding-Factor (DREB), which is interacted with cold regulated genes (*COR*) signaling pathway (Yang et al., 2019; Zhang et al., 2020). Thus, AP2/ERF, WRKY, bZIP, MYB, bHLH, C2H2, and NAC TFs regulate the expression of gene to activate cold stress-responsive genes (*CORs*), resulting in physiological responses to cold stress (Byun et al. 2015).

AP2/ERF, a key TF family in cold stress

The APETALA2/Ethylene responsive factor (AP2/ERF) is a large transcription factor (TF) family in plants involved in plant developmental processes and multiple environmental stimuli (Klay et al. 2018). The most famous family members of the AP2/ERF involved in cold stress are DREBs, also known as CBFs. CBFs act as pioneers of plant regulatory networks in response to cold stress and has homologs in many plants. Overexpression of *CBF* homologs from *Oryza sativa*, *L. perenne*, *Zea mays*, *Hordeum vulgare,* and *T. aestivum* in transgenic tobacco or *A. thaliana* have been found to increase the expression of cold-regulated genes belonging to the CBF regulon and cold/freezing tolerance (Mizuno et al. 2006; Medina et al. 2011; Rasmussen et al. 2013; Zhu et al. 2020).

Gene expression is an intricate mechanism, as well as CBFs regulatory network in the plant during cold stress (Shi et al. 2018). The role of *CBFs* in enhancing cold/freezing tolerance in plants has been well established in many species (Winfield et al. 2010; Artlip et al. 2014). CBFs activate cold stress-responsive genes through specific binding to the dehydration-responsive C-repeat (DRE/CRT) *cis*-acting element (A/GCCGAC) in RD29A promoters (Mizoi et al. 2012) to increase cold stress tolerance in plants (Hao et al. 2017). However, *CBFs* may have differential functions in cold stress response because different CBFs may activate disparate *cis*-acting elements. Transient transactivation tests have revealed that all *Vitis riparia CBFs*, except *CBF5,* can bind to DRE/CRT elements, whereas *CBF3* and *CBF4* prefer the CRT element (Carlow et al. 2017). In *Zoysia japonica*, *ZjDREB1.4* demonstrated solid transactivation activity under -8 °C treatment, but weak binding to the DRE with ACCGAC as the core sequence. The ZjDREB1.4 protein preferentially binds to GCCGAC rather than ACCGAC (Feng et al. 2019). Using a TF-centered yeast one-hybrid (Y1H) experimental system, Lv et al. (2019) showed that *BpERF13* activated the reporter gene by binding to LTRECOREATCOR15 and MYBCORE *cis*-elements under low temperature. Chromatin Immunoprecipitation-sequencing (ChIP-seq) and Chromatin Immunoprecipitation Polymerase Chain Reaction (ChIP-PCR) experiments further proved that *BpERF13* binds to the promoter of *CBF* genes as well (Lv et al. 2019).

The up-regulated capacity of *CBFs* by low temperature is related to species genotype (Sakuma et al. 2002) and might be influenced by polymorphisms within promoter sequences of plants (Pan et al. 2013). For instance, the response of a cold-tolerant cultivar is slightly slower than the cold-sensitive cultivar under cold stress in *Brassica rapa*. Three *OsCBFs* genes (*OsCBF1*-3) showed a temporary induction in the CA process (10 °C) and were much more intense in *Indica* rice (93–11 variety) than *Japonica* rice (Nipponbare variety). *OsLIP5* and *OsLIP9* (the candidate downstream genes) were induced in *Indica* rice but not in *Japonica* rice. This result indicates that polymorphisms within promoter sequences caused differential expression of CBF regulon (Pan et al. 2013).

In addition, overexpression of *CBFs* improves cold tolerance through elevating antioxidant enzymes, including catalase (CAT), ascorbate peroxidase (APX), peroxidase (POD), superoxide (SOD), and proline, and also reduce EL, MDA, $H_2O_{2,}$ and O^{2-} contents under cold stress condition (4 °C) (Sun et al. 2019; Hu et al. 2020). Li et al. (2018) used Clustered Regularly Interspaced Short Palindromic Repeats Associated Protein 9 (CRISPR-Cas9) system to generate *slcbf1* mutants. The mutants had lower proline and higher antioxidant enzyme activity compared to wild-type. The transgenic plants developed by the AP2/ERF TF family have been listed in Table 1.

CBF genes are rapidly and transiently induced by low temperature and attenuated during the later stages of the cold stress response. In *A. thaliana*, the attenuation process of *CBFs* is mediated by protein kinase Brassinosteroid-Insensitive2 (*BIN2*) under freezing assay. The *A. thaliana* seedlings were moved to 4 °C conditions for 3 d and followed by − 9 °C treatment for 0.5 h. BIN2 associates with and phosphorylates ICE1 under prolonged low-temperature stress to facilitate the interaction between the E3 ubiquitin ligase High Expression of Osmotically Responsive Gene1 (HOS1) and ICE1, resulting in degradation of ICE1 in *A. thaliana* (Ye et al. 2019). On the contrary, cold-responsive protein kinase 1 (CRPK1) which is acts as a negative cold regulator phosphorylates 14–3-3 proteins. In the cytosol, the phosphorylated 14–3-3 proteins were translocated to nucleus and in association with CBFs disturbed the key

Table 1 AP2/ERF TF genes in the transgenic plant under cold stress

No.	Gene	From	To	Other functions	Location	Homologs	Temperature and time points	Beneficial roles	References
1	*AmCBF2*	*Avicennia marina*	*A. marina*	Salt, drought, heavy metals stress	NA	NA	5 °C for 15 min, 2 h, 12 h, 24 h, 48 h, and 120 h	Involve in a cold signaling pathway	Peng et al. (2013b)
2	*GmDREB1A; 1GmDREB1A;2*	*Glycine max*	*A. thaliana*	NA	NA	NA	4 °C for 0 h, 1 h, and 24 h	Responsive to cold stress culminating	Yamasaki and Randall (2016)
3	*HvSHN1*	*H. vulgare*	*Nicotiana tabacum*	Salt, drought, and heat stress	Nucleus	*TdSHN1AtSHN1, 2,3*	4 °C for 5 d	Maintain chlorophyll content under multiple abiotic stresses	Djemal et al. (2018)
4	*PpCBF1*	*M. domestica*	*P. persica*	NA	NA	NA	NA	A modest increase in cold hardiness and induces dormancy	Artlip et al. (2014)
5	*TdSHN1*	*Triticum durum*	*N. tabacum*	Salt, and water stress	NA	NA	4 °C for 5 d	Reduce the stomatal density, and increase the expression of osmotic stress pproteins, lipid transfer proteins (LTPs), defensive proteins, genes encoding oxidative stress-related proteins, and the wax biosynthesis gene (*NtCER1*)s	Djemal and Khoudi (2016)
6	*DaCBF7*	*Deschampsia antarctica*	*O. sativa*	NA	Nucleus	NA	4 °C for 8 d	Induces diverse sets of genes and confers cold tolerance	Byun et al. (2015)
	ZjDREB1.4	*Z. japonica*	*A. thaliana*	NA	Nucleus	*DREB1*	20, 15, 10, or 6 °C for 2 h	Induces the expression of multiple genes including a part of the CBF-regulon and	Feng et al. (2019)
7	*BpERF13*	*B. platyphylla*	*B. platyphylla*	NA	Nuclei	NA	4 °C for 0, 2, 4, 6, or 12 h	Regulates physiological processes under cold stress in woody plants	Lv et al. (2019)
8	*CdERF1*	*Cynodon dactylon*	*A. thaliana*	NA	Nucleus	NA	4 °C, for 0, 1, 3,6, 12, and 24 h	Activate stress-related genes, PODs, CBF2 and LTPs	Hu et al. (2020)
9	*VpERF2*	*Vitis pseudoreticulata*	*A. thaliana*	Drought, and heat stress	Nucleus	NA	4 °C for 0, 2, 4, 6, 8, 10, 12, and 24 h	Involve in abiotic stress-responsive pathways	Zhu et al. (2013)

Table 1 continued

No.	Gene	From	To	Other functions	Location	Homologs	Temperature and time points	Beneficial roles	References
10	*CsERF*	*Citrus sinensis*	*N. tabacum*	NA	Nuclei	NA	4 °C for 0 h, 2 h, 4 h, 8 h, 12 h and 24 h	Activate four indicator genes: two cold responsive transcription factor genes (*NtCBF1* and *NtCBF3*), and two cold-induced genes(*NtERD10B* and *NtERD10C*)	Ma et al. (2014)
11	*SmCBF1, SmCBF2, SmCBF3*	*S. melongena*	*S. melongena*	Drought, high salinity, and ABA stress	Nucleus and cytoplasm	NA	4 °C for 0 h, 0.5 h, 1 h, 3 h, 6 h, 12 h, and 24 h	Involve in regulation of the response to abiotic stress	Zhou et al. (2018)
12	*VaERF080, VaERF087*	*Vitis amurensis*	*thaliana*	NA	NA	NA	4 °C for 0, 2, 4, 8, 24,and 48 h	Increase the antioxidant enzyme activities and nine representative cold-responsive Gene expressions (*CBF1*, *CBF2*, *ICE1*, *ZAT12*, *KIN1*, *SIZ1*, *RD29A*, *COR15A*, and *COR47*)	Sun et al. (2019)
13	*SmCBF*	*S. melongena*	*S. melongena*	NA	NA	NA	4 ± 0.5 °C for 12 d	Increase cold tolerance and together with eugenol fumigation reduce chilling injury	Huang et al. (2019)
14	*BjCBF*	*Brassica juncea*	*B. juncea*	NA	Nucleus	NA	4 °C for 0, 3, 6, 24 h	Binds to the DRE elements in the promoter of downstream cold-responsive genes resulting in increased cold tolerance	Kashyap and Deswal (2019)
15	*AdERF2-AdERF14*	*Actinidia deliciosa*	*A. deliciosa*	NA	NA	NA	0 °C for 12 weeks	Modulate cold stress response through changes in AP2/ERF key family expression	Yin et al. (2012)
16	*EgCBF1*	*Eucalyptus globulus*	*E. globulus*	NA	NA	NA	4 °C for 30 min	Participates in the cold-responsive pathway of *E. globulus*	Gamboa et al. (2007)
17	*MfDREB1* and *MfDREB1s*	*Medicago falcate*	*M. falcate*	NA	NA	NA	4 °C for 0 h, 0.5 h, 1 h, 3 h, 6 h and 12 h	Contribute to cold tolerance	Niu et al. (2010)
18	*PhCBF4a* and *PhCBF4b*	*Populus hopeiensis*	*N. tabacum*	Dehydration, and high salinity stress	NA	NA	4 °C for 6 h	Induce elevated expression of the CBF/DREB1 regulons without prior stimulus	Wang et al. (2014)
19	*AtCRAP2*	*A. thaliana*	*A. thaliana*	NA	NA	NA	4 °C	Promote flowering under short-day conditions	Luo et al. (2020a)

Table 1 continued

No.	Gene	From	To	Other functions	Location	Homologs	Temperature and time points	Beneficial roles	References
20	*BrcERF-B3*	*B. rapa*	*B. rapa*	Salt and plant hormone	NA	NA	4 °C for 0, 1, 2, 4, 8, and 12 h	Involve in the formation of abnormal flower and *BrcERF-B3* is more significant under cold stress in mutant plants	Xu et al. (2016)
21	*GbCBF1*	*G. hirsutum*	*N. tabacum*	NA	NA	NA	4 °C for 0, 0.25, 0.5, 1, 2, 4, 8, 16, or 24 h	Enhances cold tolerance in transgenic tobacco through reduce EL and increase proline and soluble sugar contents	Guo et al. (2011)
22	*CRF2, CRF3*	*A. thaliana*	*A. thaliana*	NA	NA	NA	1 °C for 8 h	Regulate Arabidopsis lateral root initiation under cold stress	Jeon et al. (2016)
23	*OsCBF1, OsCBF2, OsCBF3*	*O. sativa*	*O. sativa*	NA	NA	NA	5 °C for 3 d and 7 d	Transiently inducedin the process of cold acclimation to increase cold tolerance	Pan et al. (2013)
24	*SlDREB3*	*S. lycopersicum*	*S. lycopersicum*	NA	NA	NA	4 °C for 0, 3, 6, 9, 12 and 24 h	Improve the cold tolerance by upregulating *SlLEAs* expression	Wang et al. (2019a)
25	*CRF4*	*A. thaliana*	*A. thaliana*	NA	NA	NA	4 °C for 7 d	Contribute in short-term CA resulting in the enhancement of freezing tolerance	Zwack et al. (2016)
26	*FTL1/DDF1*	*A. thaliana*	*A. thaliana*	Drought and heat stress	NA	NA	−5 °C for 24 h	Regulate response to freezing stress	Kang et al. (2011)
27	*MgCBF6*	*Miscanthus giganteus*	*M. giganteus*	NA	NA	*SbCBF3, SbDBF2, SbCBF6, ZmCBF3,ZmDBF2,* and *ZmCBF6*	5 °C – (−3) °C for 3d	The dormancy strategy for overwintering	Rapacz et al. (2018)

cold-responsive CBF proteins under 4 °C for 3 h (Liu et al. 2017). Furthermore, when *A. thaliana* is imposed from 4 °C to -2 °C (2 °C per hour), the defense regulatory genes, such as *PAD4*, *SAG101*, and *EDS1* increased the freezing tolerance by enhancing CBFs and their regulons (Chen et al. 2015b).

It has been shown that *CBFs/DREBs* play a key role in *CORs* induction to increase cold tolerance in plants. Recently, it was revealed that the MEKK1–MKK2–MPK4 cascade and six additional mitogen-activated protein kinases are involved in a gene regulatory network to regulate transcription factors and cold tolerance genes in *Betula platyphylla* (Chen et al. 2021). Meanwhile, proteins involved in reducing detrimental effects associated with cold stress have also been developed and divided into three categories: signaling molecules and regulatory proteins, degradative and defensive proteins, and protective proteins. It was proved that signaling, degradative, and defensive proteins function from upstream to downstream levels and, consequently, lead to cold tolerance improvement (Kazemi-Shahandashti and Maali-Amiri 2018).

More importantly, DELLAs play a significant role in plant growth and development which is act as pivotal components of the GA signal transduction pathway in plants. DELLA genes contribute to inhibiting plant growth under cold stress (4 °C) in *Glycine soja* (Li et al. 2011). DELLAs work jointly with *CBFs* to retard plant growth. DELLAs contribute to the cold induction of *CBF1*, *CBF2,* and *CBF3* through JA signaling. In addition, *CBF3* encourages DELLAs accumulation by suppressing GA biosynthesis (Zhou et al. 2017). Taken together, JA plays a pivotal role in modulating multiple plant growth and development. It is an oxylipin compounds group that is ubiquitous in the plant kingdom (Hu et al. 2017). Low temperature-induced endogenous JA to activate *ICE1* and *ICE2*, resulting in the activation of CBF/DREB1 transcriptional cascade (Hu et al. 2013).

Hu et al. (2017) also stated that JA positively modulates the transcriptional pathway of CBF to up-regulate *COR* genes, resulting in the cold tolerance improvement. In addition, JA associates with several hormones signaling pathways including ethylene, auxin, and gibberellin to regulate cold tolerance (Liu and Timko 2021). In specific circumstances, the outcome of hormone signaling may induce *Brassinazole-Resistant 1 (BZR1)* and consequently upregulates the expression of *CBFs*. BZR1 acts as an upstream of *CBF1* and *CBF2* and directly regulates *CBF1* and *CBF2* expression to increase cold stress tolerance without affecting plant growth (Barrero-Gil and Salinas 2017). Previous findings have also shown that BZR1 regulates other *COR* genes uncoupled with *CBFs* to regulate plants response to freezing stress (−4 °C – (−7) °C) (Li et al. 2017).

It has been reported that *CBFs* expression was also influenced by several factors such as exogenous ABA, circadian clock, eugenol, and light condition under cold stress (Yang et al. 2005; Jung and Seo 2019). In *S. melongena*, *CBFs* were strongly, rapidly, and transiently induced by exogenous ABA, indicating that *SmCBFs* might be affected plant response to ABA (Zhou et al. 2018). Light signaling components like phytochrome A (phyA), phytochrome B (phyB), and Phytochrome-Interacting Factors (PIFs) are involved in the expression of *CBFs* (Xu and Deng 2020). The interaction of *CBFs* with PIF3 was assumed to attenuate the mutually guaranteed destruction of PIF3–phyB. The interaction of phyB and *CBFs* positively regulates freezing tolerance (-5 °C and -9 °C) by degrading PIF1, PIF4, and PIF5 and eventually modulating the expression of *COR* genes in *A. thaliana* (Jiang et al. 2020).

Light and cold signals were integrated and transduced by molecular regulators to downstream signaling pathways. These molecular regulators also control the transcription process of numerous cold responsive and growth promoting genes, consequently balancing plant growth and development and increasing cold tolerance. Furthermore, investigations on the effect of eugenol fumigation on the chilling injury at 4 ± 0.5 °C to *S. melongena* have revealed that eugenol treatment increased *SmCBF* expression. This finding suggests that eugenol has a potential effect on alleviating cold injury in *S. melongena* (Huang et al. 2019). In addition to *CBF* genes, Cytokinin Response Factor2 (CRF2) and Cytokinin Response Factor3 (CRF3), members of AP2/ERF, contribute to cold-responsive genes and increase the lateral root adaptation of the plant to face cold stress (1 °C) (Jeon et al. 2016).

Other cold stress-related TFs

Basic helix-loop-helix (bHLH) is eukaryotes second-largest protein family, which has important functions in plant growth, survival, and the response to multiple abiotic stresses, especially chilling and freezing stress. Many studies have revealed that MYC-type bHLH activates the expression of *CBF* genes. Overexpression of *SlICE1a*, a member of MYC-type bHLH TF in *N. tabacum*, activated the expression of *CBF3/DREB1A* and their target genes, consequently increased proline levels, sugar contents, and late embryogenesis abundant (LEA)proteins under 4 °C treatment (Feng et al. 2013). In addition, expression of *CBFs*, such as *AtCBF1-3*, cold-responsive genes (*AtCOR15A*, *AtCOR47*, *AtRD29A*, and *AtKIN1*), and stress-responsive genes *NtDREB1-3*, *NtLEA5*, *NtP5CS,* and *NtERD10C* was also significantly increased in *DlICE1* and *RmICE1*-overexpressing lines under cold stress (4 °C) (Yang et al. 2019; Zuo et al. 2019; Luo et al. 2020b).

Protein–protein interaction analysis in transgenic *N. tabacum* showed that *MabHLH1, MabHLH2,* and *MabHLH4* interacted with each other to form heterodimers in the nucleus. Indeed, those genes also interacted with *MaICE1,* an important upstream component of cold signaling. The interaction of *MabHLHs* with *MaICE1* might form a vast protein complex in the nucleus (Peng et al. 2013a). PuICE1 can physically interact with PuHHP1 protein to increase *PuDREBa* transcriptional levels under cold stress conditions (Huang et al. 2015). On the other hand, the interaction of *MYC67* and *MYC70* with *ICE1* adversely affects cold tolerance in *A. thaliana*. Overexpression of *MYC67* and *MYC70* enhanced the cold sensitivity and down-regulated the cold-responsive gene expression. The *cis*-elements in the *CBF3/DREB1A* promoter bound by MYC proteins disrupt ICE1 interaction with the *cis*-elements (Ohta et al. 2018).

The overexpression of basic leucine zipper (*bZIP*) genes and *CBFs* significantly enhanced the resistance of chilling injury and cold storage in *P. persica* (Monteagudo et al. 2018). *bZIP* genes are involved in freezing stress and act as positive regulators (Cai et al. 2018). However, *TabZIP6* has been found to negatively regulating freezing tolerance, where *CBFs* and several *COR* genes were down-regulated in *TabZIP6*-overexpressing lines by cold treatment.

Other studies also revealed that the overexpression of C2H2 Zinc finger proteins family gene *(SlCZFP1)* in transgenic *O. sativa* and *A. thaliana* induced the *COR* gene constitutive expression and increased freezing tolerance for non-acclimate transgenic plants under freezing stress conditions (Zhang et al. 2011). In banana, *MaC2H2-2* and *MaC2H2-3* were specifically induced by cold stress, which subsequently repressed *MaICE1* expression (Han and Fu 2019). Sequence analyses revealed that a CRT/DRE element was found in *ZFP245* promoter region and *ZFP182* (Huang et al. 2005, 2012).

Another TF family that contributes to cold stress is Myeloblastosis (MYB) TF. The overexpressing of *MdMYB15L* in red-fleshed apple callus prevented the expression of *MdCBF2* and resulted in decreased cold tolerance but did not give any effect on anthocyanin levels after cold treatment. ChIP-PCR and electrophoresis mobility shift assay (EMSA) analysis indicated that *MdMYB15L* binds to type II *cis*-acting element found in the promoter of *MdCBF2* under 4 °C treatment (Xu et al. 2018). A study of *MdMYB108L* expression under cold stress showed that MdMYB108L upregulated *MdCBF3* by binding its promoter region to increase cold tolerance in *M. domestica*. Conversely, the expression of *MdHY5* was significantly downregulated by *MdMYB108L* (Wang et al. 2019d). EMSA and transient expression assay proved that *MdHY5* positively regulated the transcription of *MdCBF1* by binding to the G-Box motif of its promoter (An et al. 2017). Furthermore, CBF-independent cold-regulated genes expressions were also regulated by *MdHY5* under 4 °C for ten days. Similar to *MdMYB108L*, *MdMYB73* increased the expression of *MdCBF2- MdCBF5* in transgenic *M. domestica* (Wang et al. 2019d), illustrating that *MdMYB73* enhanced cold tolerance through CBF cold response pathway under 4 °C condition (Zhang et al. 2017).

The interactions of some cold stress-related genes in plants were shown in Fig. 1. The current study identified the interaction network using STRING version 11.0 (https://string-db.org/cgi/) (STRING 2021). *AtACS2* showed co-expression patterns with other genes such as *AtERF2*, *AtWRKY46*, *AtMYB73*, *AtABF2*, and *AtRHL41*. Co-expression is the simultaneous expression of two or more genes which makes it impossible to determine whether *AtERF2* activates *AtACS2* and *AtMYB73* activates *AtRHL41*, or *AtMYB73* activates *AtWRKY46*, or whether another gene activates them in *A. thaliana* under cold stress. In addition, *RHL41* and *MYB73* were experimentally found that enhance CA and abiotic stress tolerance in plants (Iida et al. 2000; Rasmussen et al. 2013; Barrero-Gil et al. 2016).

MdMYB88 and *MdMYB124* are examples of genes that promote anthocyanin accumulation in response to cold stress. *MdMYB88*/*MdMYB124* from R2R3-MYB TF acts as a key regulator of the *MdCCA1*, which enhances the expression of *MdCBF3* under cold stress (4 °C) in *M. domestica* or *A. thaliana* (Xie et al. 2018). Interestingly, *VcMYB4a* expression in *Vaccinium corymbosum* was downregulated by cold, salt, and drought treatment, but it was induced by freezing and heating. Additionally, gene expression enhanced abiotic sensitivity under cold, freezing, heat, drought, and salt stress in *V. corymbosum* callus, illustrating that *VcMYB4a* might act as an important repressor of abiotic stress in this species (Zhang et al. 2020). *OsMYB30* down-regulated a few β-amylase (*BMY*) genes during cold stress (4 °C), bonded to the promoters of *BMY* genes and interacted with *OsJAZ9* to repress BMY gene expression (Lv et al. 2017).

Regarding the *OsMYB30*, the use of CRISPR–Cas9 significantly increases yield production and cold stress resistance in *O. sativa*. Zeng et al. (2020) used the CRISPR–Cas9 system to edit two target sites of *OsMYB30* with high efficiency 63% for OsMYB30-site1, and 58% for OsMYB30-site2. The results showed that the osmyb30 mutants exhibited enhanced cold tolerance. The study proved that cold stress resistance and high performance rice varieties can be resulted via gene-editing techniques. However, there is still little information concerning how PLANT U-BOX 25 and 26 (PUB25 and PUB26) contribute the enhancement of CBF gene expression by degrading

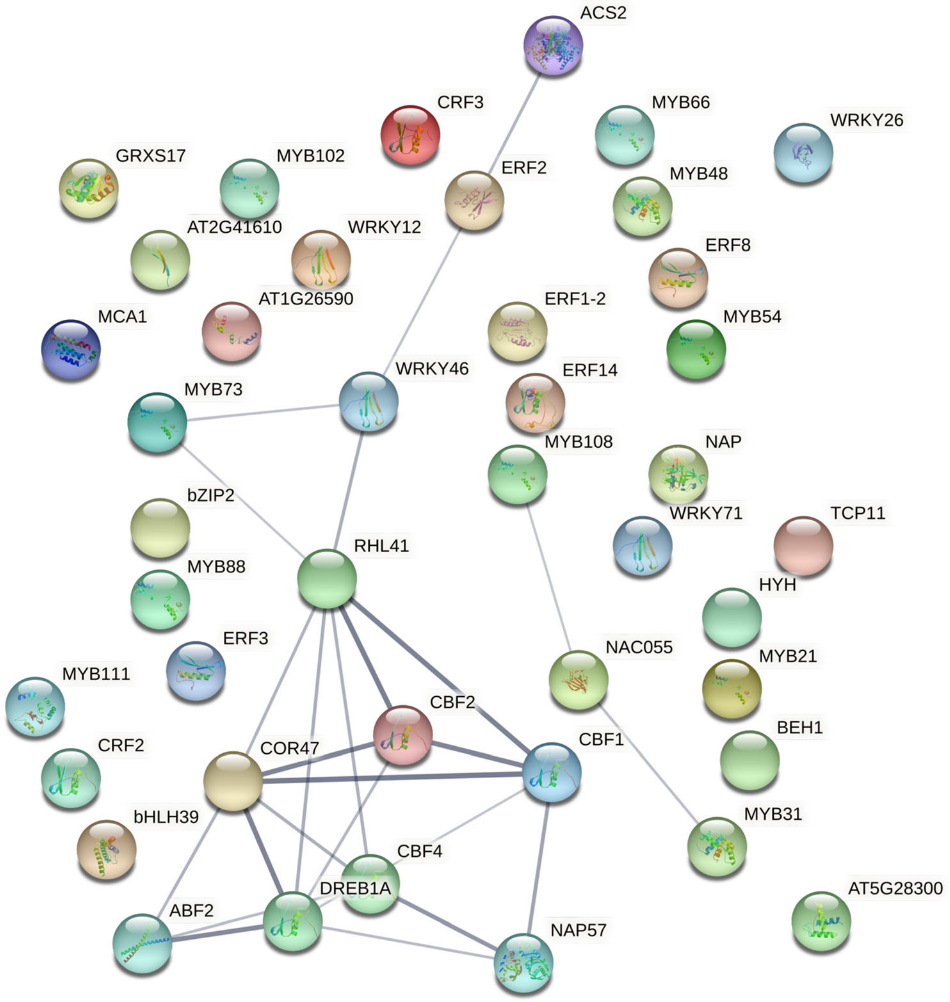

Fig. 1 Interaction network analysis of TFs genes identified in *A. thaliana* by using STRING. The interaction network has significantly more interactions than expected. This means that 42 *A. thaliana* proteins have more interactions among themselves, indicating the proteins are at least partially biologically connected as a group. The line color is related to the type of interaction. The green line shows gene neighborhood, the pink line means experimentally determined, the black line means co-expression, the dark blue line means gene co-occurrence, and the blue line means protein homology. (For more interpretation of the color codes in this figure legend, the reader is referred to the web version of this network analysis (https://string-db.org/cgi/network?taskId=btbDj6SKVsTf&sessionId=b4DLtXYWAftY)

MYB15 to improve cold tolerance in *A. thaliana* under 4 °C treatment (Wang et al. 2019c).

Meanwhile, cold signaling pathway was positively regulated by *CsWRKY46* in an ABA-dependent manner. Numerous cis-regulatory elements were found in the upstream region of WRKY genes in *C. sativus*. Phytohormones (MeJa, ABA, SA, GA, auxin, and zeatin) were associated with WRKY expression to obtain cold tolerance enhancement (Zhao et al. 2015; Govardhana and Kumudini 2020). *CsWRKY46* associates with the W-box (TTGACC/T) in the ABA-responsive transcription factor (ABI5) to increase the expression of *RD29A* and *COR47*, the member of stress-inducible genes. Consequently, *C. sativus* over-expressing *CsWRKY46* and *A. thaliana* over-expressing *CsWRKY46* had higher survival rates, higher proline accumulation, and less EL and MDA levels under 4 °C cold stress (Zhang et al. 2016). An increase in cold stress tolerance can be seen by a higher survival rate (Ju et al. 2020).

Overexpression of *SlNAM1*, a member of NAC TF family in transgenic *N. tabacum* increased minor wilting, photosynthetic rates (Pn), germination rates, and osmolytes contents under chilling stress. Reduction in H_2O_2 contents under cold stress has a pivotal role in minimizing the cell membrane's oxidative damage in transgenic *N. tabacum* overexpressed *SlNAM1*. The increased cold stress tolerance in transgenic *N. tabacum* was also assumed to increase transcripts of *NtDREB1*, *NtP5CS*, and *NtERD10s* (Li et al. 2016). Activation of the DREB/CBF–COR pathway caused by over-expression of *GmNAC20* under freezing stress may promote and control lateral root formation through auxin signaling-related genes alteration (Hao et al. 2011). Likewise, *PbeNAC1* protein associates with *PbeDREB1* and *PbeDREB2A* to enhance mRNA levels in some stress-associated genes in *P. betulifolia* under cold stress (Jin et al. 2017).

Other studies in NAC genes from *M. domestica* found that *MdNAC029* acts as a negative regulator of cold stress.

Over-expression of *MdNAC029* decreased cold tolerance in calli of *M. domestica* and transgenic *A. thaliana*. These findings were supported by EMSA and transient expression assays which illustrated that *MdNAC029* suppressed the *MdCBF1* and *MdCBF4* expression by binding to their promoters (An et al. 2018). Moreover, Liu et al. (2018b) found that *ShNAC1* has a negative role in cold stress tolerance in plants. *ShNAC1* acts as a negative regulator in cold tolerance in *S. lycopersicum* by regulating the ethylene biosynthesis and signal transduction pathways.

A potential transcriptional regulatory network, including AP2/ERF, MYB, bZIP, bHLH, and NAC, is directly associated with other gene expressions (Wang et al. 2019b). *CsLEA* (a novel gene encoding a late embryogenesis abundant protein from LEA_3 subfamily protein) was significantly induced by cold stress, illustrating that *CsLEA* associated with TFs increases cold tolerance in plants. Furthermore, it was assumed that low molecular weight and high hydrophilicity of *CsLEA1* might be related to the heterologous expression of *CsLEA1* which increased the cold stress tolerance of *Escherichia coli* and yeast (Wang et al. 2019b). *MfNAC*3, an NAC TF from *M. falcate* increased *MtICE3*, *MtCAS15,* and *MtCAS31* expression under cold treatment in *M. truncatula*. ICE1 is an important TF in regulating the expression of CBFs, while *CASs* are important regulons of CBFs. Consequently, *MfNAC3* binds to the CATGTG and CACG motifs in the promoter region of *MtCBF4* to increase cold tolerance in *M. truncatula* (Qu et al. 2016). In transgenic *A. thaliana* overexpressed *LlNAC2* from *L. lancifolium*, various stress-related cis-acting regulatory elements were demonstrated in the *LlNAC2* promoter and this promoter was able to enhance GUS activity under cold stress. *LlDREB1* and *LlZFHD4* bind and interact with the *LlNAC2* promoter to enhance stress tolerance (Yong et al. 2019). Besides the CBF-dependent pathway, NAC genes improve freezing stress tolerance through ABA-dependent pathway, a phenomenon that might be related to the enhancement of expression level of stress-responsive genes and scavenging capability of ROS (Zhao et al. 2016).

Conclusion and future perspective

Molecular approaches have been used to identify the role, function, regulation, interaction, and changes of AP2/ERF TF and other TFs under cold stress, such as transgenic breeding (overexpression and gene silencing), Y2H, EMSA, ChIP Seq, omics analysis, and CRISPR-Cas9 along with bioinformatics tools and web-based genetic database as well to improve cold stress resistance in plants (Fig. 2). Though transgenic technique promises to be a good source of cold stress resistance plant (Shahzad et al. 2021), but this technique still has several shortcomings such as unexplored metabolic pathways. Therefore, the omics analysis oupled with CRISPR-Cas9 and bioinformatics tools have been used to reveal several functional features in the plant genome to provide the best plant characteristics (Raza et al. 2021; Razzaq et al. 2021).

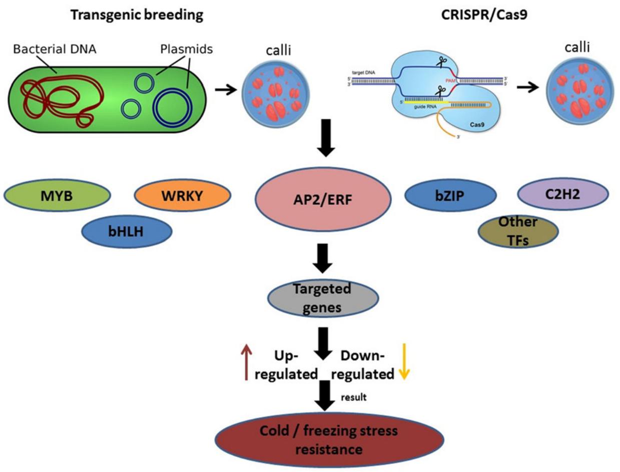

Fig. 2 Schematic illustration of improvement techniques particularly targeted modifications in TFs via transgenic breeding and CRISPR/Cas9. Different TFs that can be used for incorporation of cold or freezing stress tolerance in plants. TFs activate or modify different signal transduction pathways such as up-regulate or down-regulate targeted genes. TFs alleviate cold/freezing stress and consequently increase cold stress resistance

As shown in Fig. 3, *CBFs* (a member of AP2/ERF TF family) were activated or upregulated by the bHLH, bZIP, C2H2, MYB, WRKY, and NAC TFs. *CBFs* bind to the promoter of *COR* genes and induce the cold stress genes expression to improve cold/freezing tolerance. Contrary, TCP TF contributed to repressing *CBFs* expression resulted in reducing cold tolerance in plants. In addition, other novel genes and factors such as light, hormones, and other exogenous treatments related to cold stress are needed to improve our understanding of cold stress mechanisms in plants. The intricate physiological and molecular mechanism in plants under cold/freezing stress calls for researchers to identify other possible factors related to the cold stress mechanism. An understanding of such factors could allow scientists to identify the most

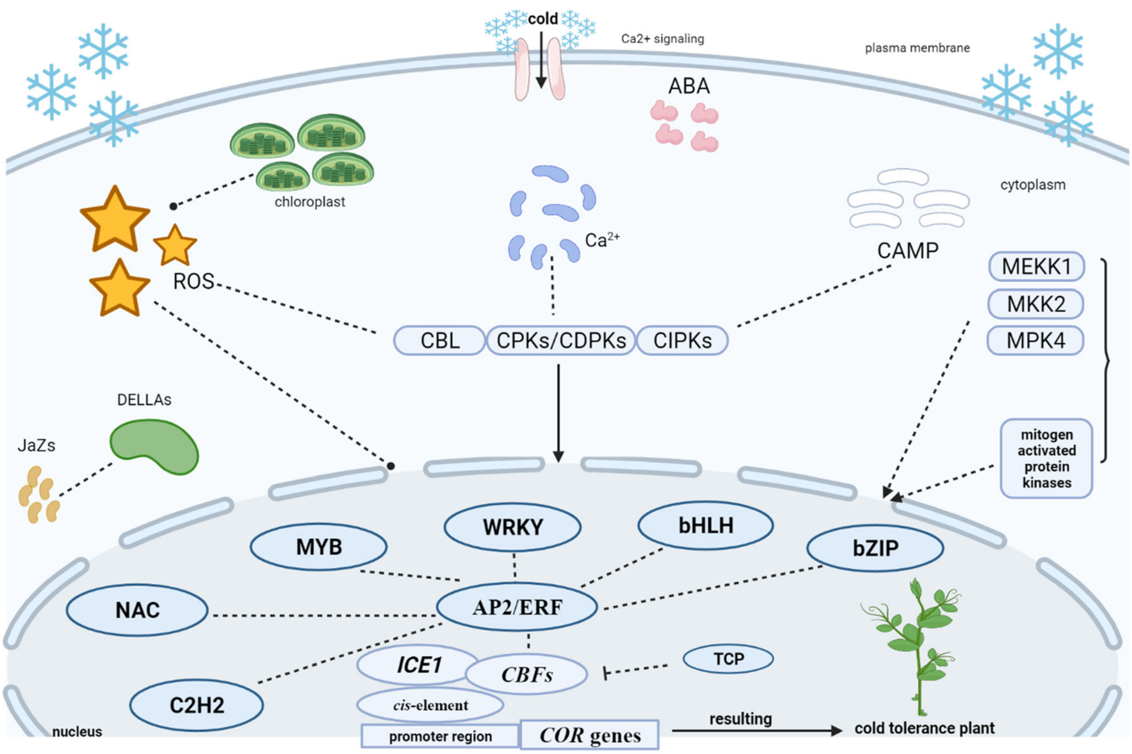

Fig. 3 The mechanism of cold tolerance in plants. Cold is sensed by receptors in the plant membrane and followed by the increase of Ca^{2+}, CAMP, ROS, and ABA as well. The chloroplast modulates the signal to the nucleus through ROS production while Ca^{2+} signaling mediates plant response to cold stress. Besides, Ca^{2+}, CAMP, and ROS signaling mediate signal transduction via CBL, CPKs/CDPKs, and CIPKs to the nucleus through a pathway mediated by ICE-CBF TFs. The MEKK1–MKK2–MPK4 cascade and mitogen-activated protein kinases also involve in the gene regulatory network to regulate TFs and cold tolerance genes. *ICE1* and *CBFs* (member of AP2/ERF TF family) are associated with the COR signaling pathway to increase cold tolerance in plants. Furthermore, WRKY, bZIP, MYB, bHLH, C2H2, NAC, and other AP2/ERF transcription factor members regulate gene expression for the activation of *COR* genes. In addition, the *CBFs* were induced by other TF families, such as WRKY, bHLH, bZIP, MYB, NAC, and C2H2. The up-regulated CBFs regulate and activate the expression of *COR* genes and resulted in improving cold tolerance in plants

suitable molecular breeding technique that can provide the best cold stress tolerance plants.

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Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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