

Molecular Basis of Soybean Cold Tolerance

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Contributor: Mesfin Tsegaw , Workie Anley Zegeye , Bingjun Jiang , Shi Sun , Shan Yuan , Tianfu Han , Tingting Wu

Cold stress is a major factor influencing the geographical distribution of soybean growth and causes immense losses in productivity. Understanding the molecular mechanisms that the soybean has undergone to survive cold temperatures will have immense value in improving soybean cold tolerance. Cold-tolerant quantitative trait loci (QTLs) were found to be overlapped with the genomic region of maturity loci of *E1*, *E3*, *E4*, pubescence color locus of *T*, stem growth habit gene locus of *Dt1*, and leaf shape locus of *Ln*, indicating that pleiotropic loci may control multiple traits, including cold tolerance. The C-repeat responsive element binding factors (CBFs) are evolutionarily conserved across species. The expression of most *GmDREB1s* was upregulated by cold stress and overexpression of *GmDREB1B;1* in soybean protoplast, and transgenic Arabidopsis plants can increase the expression of genes with the DRE core motif in their promoter regions under cold stress. Other soybean cold-responsive regulators, such as *GmMYBJ1*, *GmNEK1*, *GmZF1*, *GmbZIP*, *GmTCF1a*, *SCOF-1* and so on, enhance cold tolerance by regulating the expression of *COR* genes in transgenic Arabidopsis. CBF-dependent and CBF-independent pathways are cross-talking and work together to activate cold stress gene expression.

soybean

cold stress

CBF

molecular pathways

1. Influence of Cold Stress on the Growth and Development of Soybeans

As a major environmental factor, cold stress limits where crops can be grown and reduces yields. Cold stress reduced soybean seed yield on average by 24% compared to unaffected plants [1]. Crops like soybeans, which are native to temperate areas, need warm temperatures for germination, growth, development, and maturation. The optimum temperatures for soybean germination, flowering, and maturity are 15–22 °C, 20–25 °C, and 15–22 °C, respectively [2]. They exhibit symptoms of injury when exposed to low non-freezing temperatures. The chilling temperature affects soybean development from germination to maturity. Soybean seeds are sensitive to the chilling temperature during germination [3]. When the average air temperature drops below 15 °C, it causes growth retardation and the inhibition of new leaf and shoot production in soybean, while a drop below 10 °C may even cause them to fail to flower [4]. Chilling temperature stress during flowering has led to decreased pollen density and, consequently, decreased pod setting and a remarkable reduction in seed yield [5][6][7]. Gass and Schori [8] also reported irregular distribution of pods and seeds along the stem due to cold stress in the soybean. Inhibition of pod formation occurred when the minimum temperature of a single night dropped to 8 °C [9]. In the winter nursery of Hainan, aborted or infertile pods are common when chilling weather occurs. Cold stress prevents soybean growth by inhibiting metabolic and physiological activities, such as water uptake, cellular dehydration, and oxidative

stresses [\[10\]\[11\]](#). Aquaphotomics analysis revealed major changes in the water molecular structure in soybean leaves, as well as altered carbohydrate and oxidative metabolism in response to cold stress [\[12\]](#).

2. Candidate Genes/QTLs Associated with Cold Tolerance in Soybean

The exploitation of stress-tolerant genes and quantitative trait loci (QTLs) are effective ways to generate stress-tolerant crops [\[13\]](#). Chen et al. [\[14\]](#) have identified 422 SNPs and 302 genes associated with drought tolerance by using 136 soybean genotypes under well-watered and drought conditions. The study confirmed that these important loci and potential genes are valuable for soybean drought-tolerance breeding programs. Soybean breeders and researchers have also identified several QTLs associated with chilling tolerance. Among them, the locus *T/t* (tawny/gray pubescence) has been studied most intensively. Cultivars and lines with the *T* allele at the *T* locus, which controls the color of pubescence, have repeatedly been demonstrated to exhibit better chilling tolerance than those with the alternative allele, *t* [\[5\]\[6\]\[15\]](#). The pod settings in soybeans under short-term and long-term cold treatments were different across cultivars. An earlier study reported a strong relationship between one of the soybean genes regulated by cold (*Src2*) transcript accumulation and chilling tolerance in soybean seedlings [\[16\]](#). However, evidence showing that these loci are directly involved in chilling tolerance remains to be provided. There is also a genetic association between ascorbate peroxidase (APX1) isozyme, a ROS-scavenging enzyme, and chilling tolerance in soybeans, which shows that APX1 deficiency boosts tolerance against the chilling temperature. Although it is indicated that there is no linkage between the *apx1* locus and the previously reported loci associated with chilling tolerance, further experiments may be needed to verify its linkage relationship with recently identified QTLs [\[17\]](#). Maturity loci known to control maturity such as *E1*, *E3*, and *E4* were also found to be associated with chilling tolerance for both seed yield and quality [\[18\]](#). The *E1* allele was found to be more important than the *e1* allele in chilling tolerance [\[19\]](#). Moreover, three QTLs, *qCTTSW1*, *qCTTSW2*, and *qCTTSW3*, were detected for chilling tolerance in seed-yielding ability. The two QTLs, *qCTTSW1* and *qCTTSW2*, were mapped near the QTLs for flowering time [\[18\]](#). Stem growth habit gene (*Dt1*), regulators of leaf shape (*Ln*), and pubescence density (*P1*) loci have been associated with chilling tolerance in soybeans [\[20\]](#). Out of the five QTLs for pigmentation associated with chilling, identified by Githiri et al. [\[21\]](#), two of them, *fd2* and *fd4*, are believed to correspond to maturity genes *E1* and *E3*, respectively.

Twelve QTLs were detected for tolerance to chilling temperature during germination by one-way ANOVA. More than 28 QTLs related to cold acclimatization were identified from genome-wide studies in soybeans during germination and seedling stages. Of these, 10 QTLs were detected at both stages, indicating the possibility of developing a soybean variety of chilling-temperature tolerance for both stages using these kinds of overlapping QTLs [\[13\]](#). A QTL analysis around soybean inverted-repeat CHS pseudogene (*GmIRCHS*) showed that *GmIRCHS* or a region located very close to it was responsible for cold tolerance [\[22\]](#).

3. Soybean Cold Responsive Regulators and Associated Cold Regulated (COR) Genes

3.1. Soybean CBF-Dependent Cold Response Regulatory Pathway

The C-repeat binding factor/dehydration-responsive element binding factor (CBF/DREB) belonging to AP2/ERF family transcription factors plays important roles in cold temperature response in plants [23]. The CBF/DREB1 transcription factor can bind to the promoter's CRT/DRE (C-repeat/dehydration-responsive element) region in cold-responsive genes [24]. *AtCBFs* can function as transcriptional activators that bind to the CRT/DRE regulatory element of cold-regulated genes in Arabidopsis [25]. It has been found that *CBF* genes are conserved in plants that can or cannot acclimate to cold temperatures, including rice (*Oryza sativa*), tomato (*Solanum lycopersicum*), rapeseed (*Brassica napus*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), maize (*Zea mays*), and soybean (*Glycine max*) [25][26][27]. A total of 44 homologs of Arabidopsis CBFs have been identified from soybeans [28]. Unlike the tandem array arrangement of three Arabidopsis CBFs in the same chromosome, soybean CBF genes were duplicated and scattered among different chromosomes [28].

The expression of most *GmDREB1s* was upregulated by abiotic stresses, such as cold, salt, drought and heat stresses [29]. Seven *GmDREB1s*, *GmDREB1A;1*, *GmDREB1A;2*, *GmDREB1B;1*, *GmDREB1B;2*, *GmDREB1C;1*, *GmDREB1D;1*, and *GmDREB1D;2* were significantly upregulated after an hour and remained elevated at 24 h under cold stress [28][29]. Another soybean *DREB* gene, *GmDREB3*, was upregulated after 0.5 h of cold treatment and was not detected in 3 h after cold treatment. Overexpression of *GmDREB3* improved drought, high salt, and cold stress tolerance in transgenic Arabidopsis [30]. Overexpression of *GmDREB1B;1* in soybean protoplast can increase the expression of genes with the DRE core motif in their promoter regions under abiotic stress conditions. *GmDREB1B;1* can activate many soybean-specific cold-responsive genes including *GmPYL21*, an ABA receptor family gene, which could activate the downstream ABRE-mediated gene expression in an ABA-independent way. Soybean *DREB1s* were demonstrated to upregulate the transcription of downstream *COR* genes *AtCOR47* and *AtRD29a* and increase cold tolerance in transgenic Arabidopsis [29]. Regulated by *DREB1* genes, *GmVRN1* is strongly accumulated in the *AtDREB1A*-overexpressing soybean [31]. *GmVRN1* is responsive to low temperatures and is believed to participate in the vernalization pathway in transgenic Arabidopsis to regulate flowering time.

The soybean ethylene pathway is found to regulate the soybean CBF/DREB1 cold-responsive pathway by the accumulation of transcripts encoding the transcription factor *GmEIN3* in response to the cold [32]. *GmEIN3* inhibits the CBF/DREB1 pathway in soybeans. Transcription of soybean *DREB1A;1* and *DREB1B;1* was found to be upregulated by the cold, and their levels were consistently increased and decreased by ethylene pathway inhibitors and stimulators, respectively. Further studies would be required to determine whether *GmEIN3* negatively regulates *GmDREB1A;1* by binding to the DRE motif in the *GmDREB1A;1* promoter during cold stress.

Besides the CBF-dependent (DRE-mediated) pathway, the CBF-independent pathway, which is activated by other transcription factors rather than CBF/DREB, such as MYB, bZIP, WRKY, and Zinc Finger-type transcription factors [33][34][35][36], is also important for soybean cold-tolerance. Transcription factors in the CBF-independent pathway mostly have a cis-acting element named the ABA-responsive element (ABRE; ACGTGG/TC) in their promoter regions. The ABA-responsive element (ABRE) controls the transcription of downstream target genes through the ABRE-binding protein/ABRE-binding factor (AREB/ABF). Contrary to the belief that DRE-mediated (CBF-

dependent) and ABRE-mediated (CBF-independent) pathways are known to act in a parallel manner, the findings reveal that these pathways cross-talk and work together to activate cold stress gene expression in Arabidopsis [37]. Narusaka et al. [38] also reported that DRE-mediated and ABRE-mediated gene expressions are interdependent in the stress-responsive expression of *COR* genes like *RD29A*. Similarly, *GmDREB1B;1* directly activates *GmPYL21* expression and enhances ABRE-mediated gene expression in soybeans [29].

3.2. Other Soybean Cold Response Regulatory Pathways

Several soybean genes have been shown to mediate cold tolerance. Soybean cold-responsive genes function in multiple signaling pathways in transgenic Arabidopsis in response to chilling temperature stress in addition to the CBF-dependent pathway. Over-expression of soybean regulators, such as *GmMYBJ1* (R2R3-type *MYB* genes), *GmZF1* and *SCOF-1* (C2H2 zinc finger gene), *GmbZIP44*, *GmbZIP62* and *GmbZIP78* (bZIP transcriptional factors), *GmTCF1a* (regulator of chromosome condensation 1 (RCC1) family genes), *GmNEK1* (NEK family gene), and *GmWRKY21* (WRKY-type transcription factor) in Arabidopsis can enhance cold tolerance [33][34][35][36][39][40][41]. Most of them enhance the expression of downstream *COR* genes in a CBF-independent pathway. Different regulators induce different target *COR* genes in transgenic Arabidopsis, e.g., *GmMYBJ1* (*AtRD29b*, *AtCOR47*, *AtCOR78*, and *AtCOR15a*), *GmZF1* (*AtCOR6.6*), *GmbZIPs* (*AtERF5*, *AtKIN1*, *AtCOR78*, and *AtCOR15a*), *GmTCF1a* (*AtCOR15a*), and *SCOF-1* (*AtCOR15a*, *AtRD29B*, and *AtCOR47*).

In a CBF-independent pathway, there is a slight downregulation in the expression of *AtDREB2A* in the *GmMYBJ1* transgenic Arabidopsis, suggesting the expression of stress-responsive *COR* genes may be regulated independently of CBFs [34]. A high expression level of *GmZF1* mRNA induced by exogenous ABA suggested that *GmZF1* was also involved in a CBF-independent signal transduction pathway in transgenic Arabidopsis [40]. The ectopic expression of *GmTCF1a* does not alter the expression of *CBFs* in Arabidopsis, suggesting that the impact of *GmTCF1a* in overexpressing Arabidopsis is independent of the CBF pathway [41]. Its ortholog from Arabidopsis, *AtTCF1*, regulates freezing tolerance through a CBF-independent pathway [42].

SCOF-1, a novel cold regulator specific to soybeans, functions as a positive regulator of *COR* gene expression to enhance cold tolerance in transgenic Arabidopsis and tobacco [33]. Unlike the above common chilling response regulators, *SCOF-1* did not bind directly to CRT/DRE or ABRE in the promoter of *COR* genes; instead, it greatly enhanced the DNA binding activity of a soybean G-box binding bZIP transcription factor, *SGBF-1* [33]. Hence, the binding enhancement of *SGBF-1* by *SCOF-1* is CBF-independent in transgenic Arabidopsis. Soybean *SCOF-1* has a considerable sequence similarity with Arabidopsis *AZF* and *STZ*, which act as negative regulators of *COR* gene expression in Arabidopsis [43]. Therefore, further research can be conducted to ascertain whether *SCOF1*-like proteins are negative or positive regulators of soybean *COR* genes following cold treatments. No data was provided on the *COR* genes regulated by *GmWRKY21*. *CsWRKY46* in cucumber and *WKRY6* in Arabidopsis were found to participate in cold response in the non-CBF module [44]. However, whether *GmWRKY* interacts with *CBF* and the DRE-cis-acting promoter region is yet to be explored.

Concerning soybeans' ability for cold acclimation, an acid dehydrin family member *COR* gene, *GmERD14*, was identified from soybeans and characterized for its response to cold stress. There was little to no cold-responsive accumulation of dehydrins in soybean compared to that in cold-tolerant and cold-acclimating plants [45]. The lack of cold stress-regulated acidic dehydrin expression may contribute to the mildly cold acclimation of soybeans. At the protein level, chilling acclimation-related proteins were characterized based on the protein synthesis profile during soybean chilling treatment. Molecular characterization of the protein associated with chilling adaptation indicated that one of the members in the heat shock protein 70 (HSP70) family may enhance the capacity of soybeans' chilling acclimation [46].

Several studies conducted on soybeans have shown that Circular (circRNA)- and MicroRNA (miRNA)-based gene regulation were also involved in coordinating soybean responses to cold stress in post-transcriptional regulation [47][48][49][50][51][52][53]. In cold-treated soybean plants, miR166u, miR171p, miR2111f, and miR169c may regulate different targets in mature nodules through mRNA degradation [47]. Under chilling stress, Xu et al. [49] identified 51 miRNAs differentially expressed between chilling stress and control conditions in vegetable soybeans and indicated a negative relationship between the miRNAs and their targets. The recent finding indicates that soybean circRNAs might encode proteins and be involved in regulating low-temperature responses [51]. Kuczyński et al. [50] have identified target genes of five cold response-associated miRNAs and uncovered the nature of the correlation between target genes and the miRNAs. Transcription factors involved in cold stress response, such as *GAMYB* and *TCP*, are identified as possible targets of miR319 in Arabidopsis [53]. In contrast, *SBP-F*, *NAC-F*, and *NFY-F* are target genes of miR156a, miR164a, and miR169e in vegetable soybeans, respectively [49].

As indicated above, homolog regulators identified in the soybeans exhibited a typical function of cold responsiveness in transgenic Arabidopsis. Nevertheless, it remains to be determined whether the regulators interacted with CBF and whether they are involved in the DRE-mediated or ABRE-mediated pathways. Arabidopsis cold responsive regulators including ICE1/2, CAMATA1-5, CESTA, BZR1/BES1, CCA1/LHY, SIZ1, CRLK1/2, OST1, EBF1/2, BTF3s, PIF3/4/7, 14-3-3s, CRPK1, EIN3, PRRs, MYB15, MPK3/6, phyB, and HOS1 regulate *COR* gene expression in CBF-dependent manner. Some of them (ICE1/2, CAMATA1-5, CESTA, BZR1/BES1, CCA1/LHY, SIZ1, CRLK1/2, OST1, EBF1/2, and BTF3s) have positive effects, while other (PIF3/4/7, 14-3-3s, CRPK1, EIN3, PRRs, MYB15, MPK3/6, phyB, and HOS1) have negative effects on CBF expression [54]. *GmEIN3*, a homolog of Arabidopsis *EIN3*, was identified to be involved in soybean cold response in a CBF-dependent manner and negatively regulate *GmDREB1* expression in transgenic Arabidopsis. Moreover, Arabidopsis regulators such as SAG12, WRKY33, ERF5, CZF1, RAV1, CZF2, MYB73, ZAT10, HSFC1, NPR1, HSFA1, RCF1, STA1, HOS15, GCN5, and HD2C were involved in cold stress response through CBF-independent pathway [54]. Similarly, soybean regulators GmMYBJ1, GmZF1, GmTCF1a, and SCOF-1 were identified to regulate cold responses in transgenic Arabidopsis in a CBF-independent pathway. A comparison of regulators in soybeans and Arabidopsis showed that, although different chilling temperature responsive regulators in soybean have been reported to regulate cold response in transgenic Arabidopsis, only a few of them were studied in detail to show the exact mechanism. Even though it requires further dissection for a precise understanding, the function of soybean cold-

responsive regulators and associated *COR* genes studied in *Arabidopsis* shed light on the molecular mechanism of the cold response in soybeans and other crops.

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