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Identification, Analysis, and Functional Verification of Key Genes Under Low-Temperature Stress in Cabbage

Jin Wang[1,†,*], Oluebube Aguosuo Nora[1], Asghar Abbas[2,†], Qianzhu Wan[1], Muhammad Amir Zia[3], Martin Howard[4], Wenlong Jiang[1], Hasan Huseyin Atar[6], Mushtaq Ahmad[5] and Qinxue Zhang[1,†,*]

[1]*School of Life Sciences, Jiangsu University, Zhenjiang 212013, China*

[2]*Institute of Botany, Bahauddin Zakariya University, Multan 60800, Pakistan*

[3]*National Institute for Genomics and Advanced Biotechnology, National Agriculture Research Centre (NARC), Islamabad, Pakistan*

[4]*The John Innes Centre, Norwich Research Park, Norwich, NR4 7UH, UK*

[5]*Biodiversity and Bioenergy Research Centre, Department of Plant Sciences, Quaid-i-Azam University Islamabad, 45320, Pakistan*

[6]*Ankara University Faculty of Agriculture, Ankara Turkiye*

[†]*These authors contributed equally to this work*

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***Corresponding author:** Jin Wang & Qinxue Zhang, School of Life Sciences, Jiangsu University, Zhenjiang 212013, China

Mushtaq Ahmad, Biodiversity and Bioenergy Research Centre, Department of Plant Sciences, Quaid-i-Azam University Islamabad, 45320, Pakistan

Abstract

Plants due to their sessile nature, are continuously exposed to fluctuating environmental conditions, among which low-temperature stress is one of the most critical factors limiting growth, development, productivity, and geographical distribution of crops. In Brassica species, including Chinese cabbage and related vegetables, cold stress induces profound physiological, biochemical, metabolic, and molecular changes. These responses encompass alterations in photosynthesis, membrane stability, antioxidant enzyme activities, phytohormone signaling, and the accumulation of protective metabolites, including anthocyanins, flavonoids, glucosinolates, and osmolytes. At the molecular level, complex regulatory networks involving transcription factors (CBF/DREB, MYB, bHLH, WRKY, bZIP), hormone signaling pathways (ABA, GA, BR, SA), epigenetic regulation, non-coding RNAs, and stress-responsive genes (COR, LEA, GST, HD-ZIP, nsLTPs) coordinate cold acclimation and tolerance. Advances in genomics, transcriptomics, and functional gene analysis have significantly enhanced the understanding of cold stress responses in Brassica, revealing key pathways such as ICE-CBF-COR and MBW-mediated anthocyanin biosynthesis. This review synthesizes current knowledge on the physiological and molecular mechanisms underlying cold stress tolerance in Brassica crops, highlighting their implications for crop improvement, yield stability, and nutritional quality under changing climatic conditions.

Keywords: Cold stress; Brassica rapa; Chinese cabbage; Abiotic stress tolerance; Anthocyanins; Transcription factors; Phytohormones; Ice–Cbf–Cor Pathway; Glucosinolates; Cold acclimation

Abbreviations: MDA: Malondialdehyde; SOD: Superoxide Dismutase; APX: Ascorbate Peroxidase; CAT: Catalase; POD: Peroxidase; GPX: Glutathione Peroxidase; GBA: Glycine Betaine; ABA: Bscisic Acid; anl: Anthocyaninless; GA: Gibberellin; GA3: Gibberellin A3; TFs: Transcription Factors; lncRNAs: long non-coding RNAs; GB: Glycine betaine

Introduction

Plants interact with the environment and any conditions that exceed the limits where plants normally function may impose stress and limit plant growth and development [1]. Unlike other organisms that can avoid and protect themselves from stressful conditions through movement, plants have developed different tolerance or adaptation mechanisms that allow to defend themselves against stressors and support their growth and development [2]. Due to their sessile lifestyle plants are especially exposed to environmental changes that modulate their growth and development. Optimal plant growth takes place within more or less strict environmental conditions [3]. Outside this optimal range, plants suffer stresses that limit their growth and productivity. In agriculture some of these abiotic stresses can be minimized by using irrigation and fertilization [4]. Other stresses, however, are difficult to overcome and fluctuations in air temperature are a clear example. Variations in temperature are one of the principal factors that drive plant phenology. Stratification and vernalization are well known physiological processes that are triggered by transient exposure to low temperatures [5]. Low-temperature stress was also shown to influence specialized metabolism in Brassica plants. For example, flavonoids and anthocyanins were reported to accumulate in response to cold and frost stress in Brassica rapa [6]. While low-temperature stress leads to the accumulation of specific flavonol glycosides and hydroxycinnamic acid derivatives in Brassica oleracea var. sabellica [7].

BrANS1, BrANS3, BrDFR2, BrDFR4, BrDFR8, and BrDFR9 only showed very high responses to cold stress in pigmented B. rapa samples, while BrANS2, BrDFR1, BrDFR3, BrDFR5, BrDFR6, and BrDFR10 responded to cold and freezing stress treatments [8]. Molecular studies have revealed that the ABA-independent pathway is also crucial for stress tolerance in plants. Dehydration-responsive element binding protein 1 (DREB1)/C-repeat binding factor (CBF) and DREB2 are primarily involved in responding to cold and heat stresses, respectively [9]. Several proteins, such as ICE1, ZAT12, CAMTA3, and MYB15, have been identified as regulators of DREB1/CBF genes [10]. The anthocyanin biosynthetic genes C4H, F3H, DFR, ANS, and UFGT were enhanced under low temperature treatment [11]. Low-temperature treatment during the growth process can induce the synthesis of anthocyanins, thereby increasing their nutritional quality, ornamental appearance, and cold tolerance. A highly inbred line, Xiao Baojian' (XBJ), was utilized to investigate the anthocyanin regulation pathway and its associated genes under low-temperature stress. Consistent with previous studies, low temperature caused the leaves of Chinese cabbage to gradually turn purple [12]. Interestingly, BZR1 (Brassinazole resistant 1), an important transcription factor for BR signaling, can bind directly to the promoter regions of CBF1 and CBF2 (CBF/DREB) and promote their expression in response to low-temperature stress, further illustrating the promotion of BR signaling for low-temperature resistance (Figure 1) [13].

The 17 different S-nitrosylation sites were identified in low-temperature-stressed Brassica juncea [14]. In addition, the content of SNO under low-temperature stress was significantly increased by 1.4 times at 1 h. Low temperatures affect the photosynthesis of plants, reducing their photosynthetic efficiency [15]. Low temperature is a major environmental factor that limits plant growth, development and geographical distribution [16]. and may significantly reduce crop yields, including vegetable crops. Cabbage (Brassica oleracea var. capitata L.) is a widely distributed cruciferous vegetable crop in the world. If cabbage encounters low temperatures before the heading stage, or seedlings meet their vernalization conditions, afterwards, they are easy to bolt in the long daylight, resulting in the failure to form tight and leafy heads, which serve as a storage organ and edible product. If the temperature is lower than the tolerance of cabbage, the seedlings will freeze to death, resulting in serious economic losses. In Arabidopsis, the overexpression of miRNA156 causes delayed flowering at lower ambient temperatures, which is probably associated with the reduced levels of SPL3 mRNA [17]. MADS-box genes play an important role in many aspects of plant development [18]. MADS-box genes were initially identified as floral homeotic genes and are among the most extensively studied transcription factors (TFs) involved in developmental control [19]. The cold-resistant variety known as Longyou-7 has demonstrated its ability to survive extreme temperatures as low as 30 C, indicating the presence of numerous cold-resistance genes within it [20].

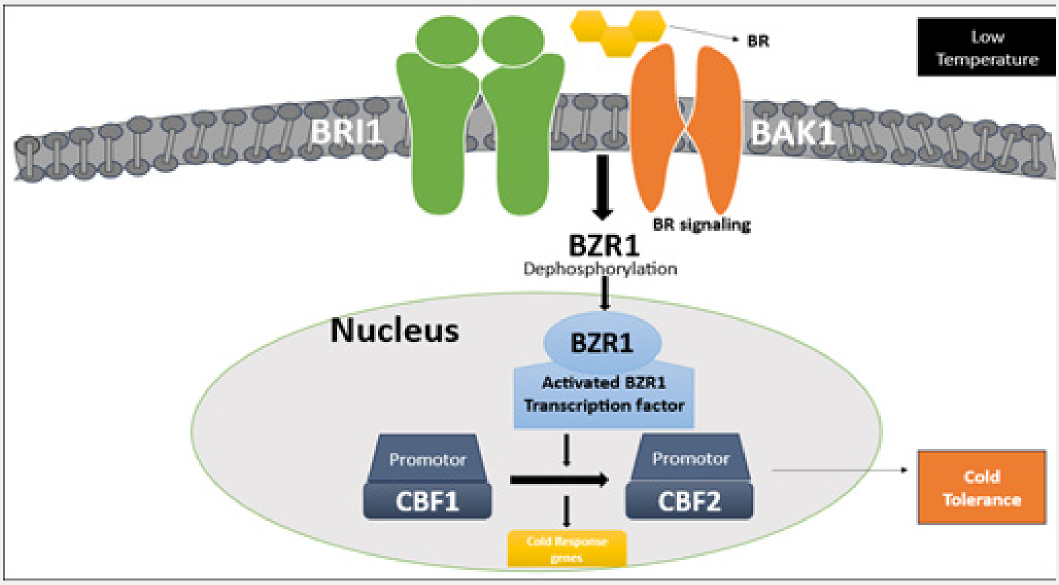

Figure 1: Low temperature activates BR signaling through BR1 and BAK1, leading to activation of Transcription factors BZR1.

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Cold stress has been found to have a significant impact on various aspects of plant physiology, biochemistry, metabolism, and molecular processes, ultimately affecting plant growth and development [21]. Cold-tolerant varieties exhibited elevated GST enzyme activity and increased expression levels of 28 stress-related genes in response to low-temperature stress. Certain CmGSTs, specifically those classified as Tau, Phi, and DHAR, were found to play a crucial role in response to cold stress. The study suggests that the JrGSTU1 transgenic walnut has the potential to enhance its cold tolerance by upregulating the expression of the GSTs gene and increasing GST enzyme activity under cold stress conditions [22]. Low-temperature stress was also shown to influence specialized metabolism in Brassica plants. For example, flavonoids and anthocyanins were reported to accumulate in response to cold and frost stress in Brassica rapa [6].

While low-temperature stress leads to the accumulation of specific flavonol glycosides and hydroxycinnamic acid derivatives in Brassica oleracea var. sabellica [7]. Plant response to abiotic stress may involve the induction of biosynthesis of various metabolites (polyphenolic compounds, carotenoids, glucosinolates) that are beneficial to human health. Kale (B. oleracea var. acephala) is tolerant to low temperatures, and in culinary practice it is considered to have the best organoleptic properties when harvested late in the growth season, after exposure to low temperatures and frost [23]. In response to low temperatures, Chinese cabbage undergoes biochemical changes, resulting in the increased production of protective compounds, including antioxidants and glucosinolates, which contribute to enhanced nutritional properties [24]. Vernalization up regulated the transcription of floral transition and glucosinolate (GSL) pathway genes and modulated glucosinolate biosynthesis in B. rapa, suggesting that GSL biosynthesis pathway is important for cold stress response in Chinese cabbage (Table 1) [25].

Table 1: Physiological, Biochemical, and Associated Molecular Responses of Brassica Crops to Low Temperature Stress/Chilling.

Brassica Species	Responses	Key Regulating Genes	Biological Significance	References
Brassica napus	Increased ROS (H2O2) & MDA, activation of antioxidant enzymes	SOD, POD, CAT gene family; BoFBX (F-Box protein positively regulates tolerance)	Antioxidant system is the primary defense against oxidative damage, F-box proteins modulate stress signaling.	[38;40]
Brassica napus/ B. rapa	Accumulation of osmolytes (Proline, Soluble Sugars)	P5CS (Proline biosynthesis)	Maintains a cell turgor, stabilizes proteins and acts as a ROS scavengers	[2;24]
Brassica oleracea (cabbage)	Reduction in photosynthesis; growth inhibition	BoPYL8 (ABA receptor); BoARR-B transcription factors.	ABA signaling (BoPYL8) and Cytokinin response regulators (BoARR-B) are crucial for transducing cold signals to growth	[40 ; 69]
Brassica oleracea (mustard)	Membrane damage	Fatty acid desaturase (FAD) genes; ELIP (Early Light induced proteins) genes.	Alteration in membrane lipid composition and protection of photosynthesis apparatus are critical for stability.	[25]
Brassica rapa	Chlorophyll resuction, Anthocyanin acuumulation	BrTT8. BrMYB2 (TF regulators), BrDFR, BrANS (Anthocyanin genes)	Trade of: Chlorophyll degradation reduces photo-oxidative risk, Anthocyanin acts as antioxidant and light screens.	[68;12]
Brassica rapa	General stress responses and signaling.	BrCCT gene family (e.g., BrCCT1); various F-box genes.	CCT proteins integrate environmental signals (light, temperature); F-box proteins control protein turnover in stress pathways.	[32 ; 31]

HD-ZIP genes participate in cold stress response by regulating cell membrane stability and ROS scavenging [26]. Brassica rapa is one of the most economically important vegetable crops worldwide. The whole-genome sequencing of B. rapa (Chiifu-401-42), conducted by the Brassica rapa Genome Sequencing Project Consortium (2011), enables us to undertake the genome-wide identification and functional analysis of gene families related to the morphological diversity and agronomic traits of Brassica crops [27]. Furthermore, B. rapa serves as a crucial reference for understanding polyploidy-related crop genome evolution because of its agronomic importance and phylogenetic relationships [27]. Crop yields are negatively affected by cold stress, including chilling (0~12°C) and freezing stress (≤0°C), resulting in constrained sowing time, damage to plant tissues, and stunted plant growth [28]. Plants respond to cold stress through a series of physiological adaptations, including regulation of phytohormones (e.g., abscisic acid, brassinosteroids, and jasmonic acid) [29].

Plants employ a range of strategies to cope with environmentally induced stresses, in which phytohormones play crucial roles [30]. Using RNA-seq, comprehensive analyses of heat treatments in NHCC identified 9,687 novel long non-coding RNAs (lncRNAs) under heat stress in B. rapa [31]. Moreover, due to promoter demethylation, high BramMDH1 expression was exhibited in cold-acclimated B. rapa and the overexpression of BramMDH1 enhanced heat-tolerance and the growth rate in Arabidopsis [32]. Plants undergo a series of physiological and morphological changes to cope with cold stress including increasing malondialdehyde (MDA) content, membrane permeability, proline accumulation, and altering antioxidant enzymes including superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), peroxidase (POD) and glutathione peroxidase (GPX) activities; such effects are generally achieved through significant transcriptional regulation [33]. Plants from temperate regions can improve their FT upon exposure to cold temperatures through a process called cold acclimation [34].

This proposes that the exogenous application of compatible solutes/osmolytes could potentially be one of the intervention strategies to improve plants' FT. Glycine betaine (GB) is one of such osmolytes that play an important role in cellular osmotic adjustment, which is associated with improved freezing tolerance through increase in resistance to freeze-induced dehydration/desiccation [35]. Numerous studies have also noted that SA treatment enhanced plant stress tolerance against abiotic stresses such as ozone, heat, salinity, chilling, and drought [36]. In addition to the physiological responses to cold and heat, plant resistance to stress is often activated by alterations in gene expression. Transcriptomics is used to evaluate systematic changes in gene expression and estimate the response of plants to temperature stress. The positive roles of high COR gene expression and the conserved mechanism of circadian clock-related genes in tobacco's response to cold stress have provided valuable insights for crop improvement under cold stress [37]. Previous studies have shown that calcium ions regulate enzyme activity in plants, including synthesis, secretion, and promotion of metabolic reactions, which helps maintain normal plant metabolism, growth, and development, as well as aiding resistance to environmental stresses such as drought, salinity, and low temperatures [38]. Among the families of transcription factors related to plant stress resistance, there are four significant categories of bZIP, WRKY, AP2/EREBP and MYB (Figure 2) [39].

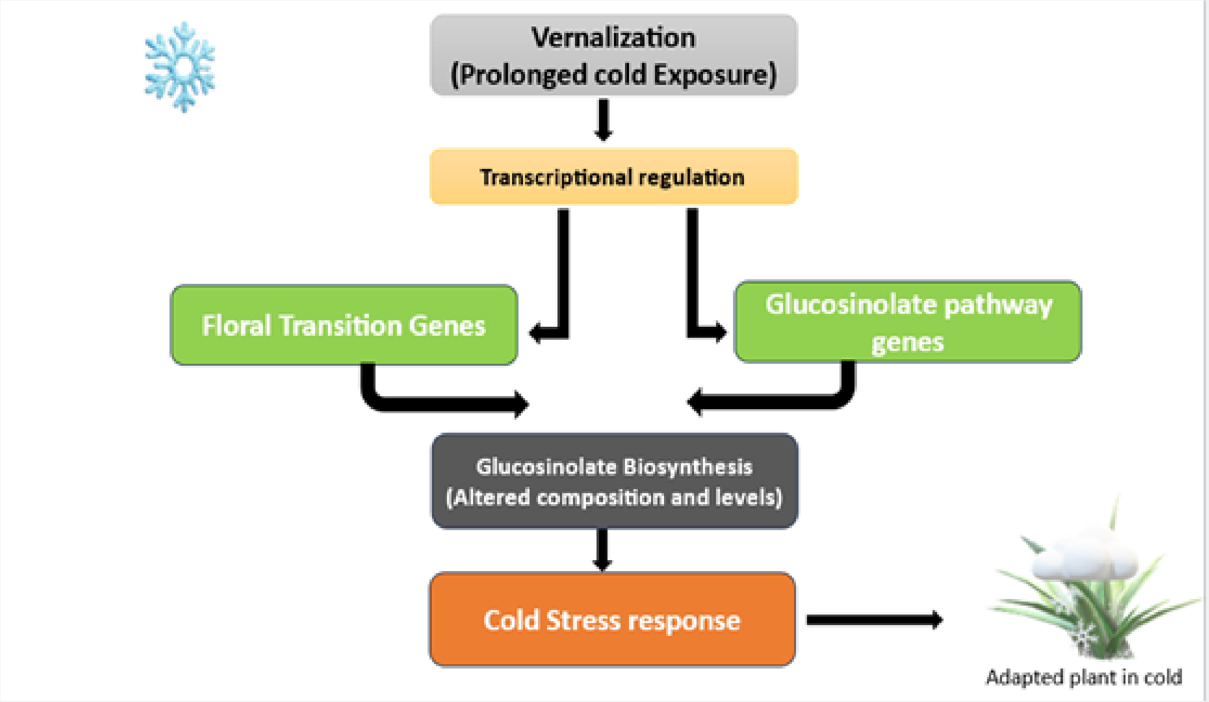

Figure 2: Vernalization mediated regulation of glucosinolate biosynthesis in Chinese cabbage.

Organisms are exposed to daily environmental cycles of light and temperature. These 24 h cycles trigger an endogenous biochemical oscillator known as the circadian clock in almost all living organisms [40]. This circadian clock coordinates internally generated rhythmic behaviors and biological processes, functioning to anticipate environmental changes associated with the day–night cycle [41]. The B. rapa Chinese cabbage is a plant belonging to the polyploid genus Brassica, and along with bok

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choy, turnip, and broccoli to, it is an important agricultural crop worldwide. After multiple genome duplications and diplidization, circadian clock genes were preferentially retained relative to their neighboring genes in the B. rapa genome [41]. The expression levels of BrSRO genes in leaves were analyzed under abiotic stresses for 24 hours, 48 hours, and 72 hours. Our results showed that the responses of BrSROs were different among heat, low temperature, drought, and salt stresses. BrSRO8 is sensitive to high temperatures, and the expressions of BrSRO1, 3, 7, 8, and 9 were higher under low-temperature treatment. The responses to drought stress were mediated by BrSRO1, 5, and 9, while those to NaCl stress were mediated by BrSRO7 and BrSRO8.

The expression level changed over time; it may be that plants regulate themselves to resist changes in the external environment. Interestingly, the expression levels of all 12 genes were upregulated after 24 h of salt treatment, indicating that all the genes responded to salt stress within 24 h. Excess salts in soils cause growth arrest, molecular damage, and even the death of many of the salt-sensitive crop species that are grown today [42]. Many important yield-related agronomic traits vary greatly among different Chinese cabbage varieties after a long period of evolution and breeding. QTL analysis, as a powerful tool, has been performed to identify candidate genes responsible for the morphological diversity of Chinese cabbage [43]. In plants, the roles of GLY systems in resistance to biotic and abiotic stresses have garnered increasing attention recently. The role of GLY systems in resisting salt, extreme temperature and heavy metal stresses was reported [44]. GLYI and GLYII can be induced by stresses at transcription and translation levels. For example, in Brassica juecea, GLYII expressions were significantly regulated under zinc stress [45].

The GLYI protein in rice roots at the seedling stage was significantly induced by low temperature stress [46]. A greater expression of LEA proteins is essential for plants to maintain normal life activities during growth or under abiotic stress-related processes. It has been demonstrated that LEA genes are upregulated in response to abscisic acid (ABA) treatment, indicating their association with ABA-related pathways [47]. 82 BrLEA gene members were identified by analyzing the genome data of Chinese cabbage. Among them, BrLEA73 belongs to the LEA-6 subfamily, for which there is less research available. Research on Caragana CkLEA6_1 found that the expression level of this gene changed significantly under low temperatures [48]. which is consistent with the results of this study. This indicates that BrLEA73 responds to low temperature stress in plants and enhances plant tolerance (Table 2).

Table 2: Anthocyanin Biosynthesis Genes and Regulators Induced by Low Temperature in Brassica.

Gene	Enzyme	Brassica Specie	Response	Reference
BoMYB2	Transcription factor (MYB family)	Brassica oleracea var. acephala (purple kale)	Directly activates anthocyanin structural genes	[11]
BrTT8	Transcription factor (bHLH family)	Brassica rapa (Chinese Cabbage)	Up-regulates the part of MBW activation complex with MYB	[69]
BrDFR	Dihydroflavonol 4-reductase	Brassica rapa (Chinese cabbage)	Significantly up-regulated, key commitment step	[12]
BrANS	Anthocyanin synthase	Brassica rapa	Markedly induced produces colored anthocyanidins.	[8]
BrUFGT	UDp-glucose; flavonoid 3-O-glucosyltransferase	Brassica rapa	Up regulated; stabilizes anthocyanin via glycosylation.	[69]
BrCHS	Chalcone synthase	Brassica rapa	Up regulated; first committed step for flavonoid pathway.	[12]
BrF3H	Flavonone 3-hydroxylase	Brassica rapa	Up regulated; early pathway enzyme.	[10]
BnaANS	Anthocyanin synthase	Brassica napus (Purple)	Correlated with tissue specific anthocyanin accumulation.	[20]
BoPYL8	Abscissic acid receptor	Brassica oleracea (Cabbage)	Induced by cold, its over expression enhances anthocyanin content and cold tolerance	[70]

The nsLTPs play critical roles in plant responses to abiotic stresses, e.g., cold, heat, salt and drought, as well as biotic stresses, e.g., bacterial and fungal pathogens [49]. Plant trichomes often secrete and synthesize different types of defense substances, such as terpenoids, amino acids, phenylpropanes, lipid derivatives. These secondary metabolites can protect plants from both biological and abiotic stress, playing a crucial role in defense. Phenylalanine, tryptophan, and tyrosine are all aromatic amino acids, among which tryptophan is the precursor of auxin, alkaloids, indoline, and plant antitoxin, while tyrosine is the precursor of isoquinoline alkaloids, betaine, and quinones [50]. Phenylalanine is the precursor of the phenyl cyclopropane pathway, and p-coumaryl coenzyme A is the intermediate of the phenyl-propane metabolic pathway, as well as the precursor of various substances such as phenylpropylene and flavonoids [51]. Chinese cabbage is a cool season crop, an overly low temperature or an extended period of low temperature would still cause harm to Chinese cabbage. In the growth cycle of plants, the reproductive growth

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stage is the most vulnerable to temperature, encompassing the formation of reproductive organs, flowering, fruit-bearing, and seed maturation. Once they encounter a low temperature, the yield of the crops will be seriously affected [52].

A low temperature would increase the activity of the antioxidant enzymes [52]. when it encounters a low-temperature environment, and many genes related to cold tolerance such as CBFs, ICE1, and WRKYs have been identified [53]. Abscisic acid plays a crucial role in the processes of plant resistance and adaptability to various abiotic stress conditions. Additionally, ABA plays a crucial role in various physiological processes, including seed formation, dormancy, germination, and reproduction. Moreover, ABA regulates reactions to environmental stresses, including heat, cold, salt, drought, and excessive levels of radiation [54]. The gene function of S3 (CT001_A03119840) was identified as abscisic acid 8'-hydroxylase. Abscisic acid (ABA) is involved in numerous processes related to environmental stress responses, as well as growth and development. Abscisic acid 8-hydroxylase is a key enzyme to regulate ABA [55]. Whole-genome duplication provides a rich genetic material for the expansion of gene families or the evolution of new genes in plants [56].

The analysis of cis-acting elements within the promoter region of the citrus SNAT gene revealed the presence of 32 distinct types of elements associated with growth and development, hormone responsiveness, and stress response. In flowering Chinese cabbage, the BcSNAT1 promoter also exhibited a high density of cis-acting elements responsive to phytohormones (including auxin, GA, MeJA, salicylic, and abscisic acid), stress (such as anaerobic induction, defense and stress responses, light, low temperature, and drought inducibility), and development (meristem) [57]. Investigation of transcriptional alterations of plants during cold acclimation is crucial for understanding the underlying molecular mechanism under LT stress. Until now, a significant number of cold responsive genes have been identified and several gene regulated networks have been reported. Among these, ICE-CBF-COR is one of the most wildly reported pathways. In most plant species, the ICE-CBF-COR pathway is induced by LT stress and then activates the appropriate expression of downstream genes, which encode osmoregulation substances [58]. Some of the cold-responsive genes have an ABA responsive element and dehydration responsive element in their promoter regions [59].

A number of studies suggest that ABA can induce increases in the transcript levels of CBF genes, perhaps via binding to the CRT/DRE element. It has the potential to encourage CBF activation. In addition, AtHAP5A regulates freezing stress tolerance through binding to the CCAAT motif of AtXTH21 in Arabidopsis. AtHAP5A and AtXTH21 overexpressing plants were more tolerant of freezing stress but less susceptible to ABA than WT plants [60]. The regulation of GAox expression has also been explored in multiple species. Research has found that GAox plays an important role not only in development and growth but also in the response to stimulation by different exogenous hormones and abiotic stresses [61]. GAox belongs to the 2OG-Fe (II) oxygenase superfamily, which is divided into multiple small families based on structural and functional differences [62]. Brassica plants, including B. Juncea, B. Oleracea and B. napus, and B. rapa, are globally important crops known for their diversity. Chinese cabbage, a B. rapa subspecies, is particularly valued for its economic and nutritional value to humans. However, it is subject to various biotic (e.g., fungi, bacteria, viruses, and insects) and abiotic stresses (e.g., low temperatures, salt, and drought) in its natural environment. This leads to severe growth stagnation, yield loss, and quality reduction of Chinese cabbage crops [63].

BrBASS7 harbors great potential for regulating cold stress. The RT-qPCR showed that this gene's relative expression fell considerably under low temperature stress. Analysis of the promoter elements revealed that BrBASS7 contained a low-temperature response element, an abscisic acid response element, and an auxin-responsive hormone response element. When plants are exposed to cold conditions, stomatal opening in their leaves is inhibited, resulting in the accumulation of ABA during stomatal closure that in turn enables plants to cope with cold stress [64]. Research has confirmed that the synthesis of GLS in Brassica plants was also affected by ambient temperature, in that low temperatures promoted the production of GLS in response to external factors [65]. Brassica contains many vegetables rich in anthocyanins. In Brassica species, numerous studies have focused on identifying genes associated with anthocyanin accumulation and their subsequent functional analysis. In rapid cycling B. rapa, an anthocyaninless (anl) locus, which inhibits anthocyanin synthesis, had been mapped to R9 [66]. BrPur, a single dominant gene controlling endophytic leaf anthocyanin accumulation in Chinese cabbage, had been mapped to linkage group A07 [67]. Additionally, numerous genes related to anthocyanin accumulation have been identified and cloned. For example, low-temperature treatment induced the expression of BoTT8 and BoMYB2/BoPAP1, regulating the accumulation of anthocyanins in purple kale [11]. The low-temperature induction of anthocyanin biosynthesis in Brassica species is achieved mainly by a core transcriptional activation complex and the induction of structural pathway genes. This induction is mediated by the activation of specific transcription factors, with MYB proteins acting as master regulators. For example, BoMYB2 (also referred to as BoPAP1) from purple kale (Brassica oleracea var. acephala) is strongly induced by cold and directly binds to the promoters of anthocyanin biosynthetic genes to activate their expression (Table 3) [11]. MYB factor BoMYB2 itself does not act alone but exerts its function within the well-characterized MBW complex, which requires interaction with a bHLH partner. Similarly, in Chinese cabbage (Brassica rapa), the bHLH transcription factor BrTT8 is upregulated by low temperature and is required for the formation of this active complex [68]. The activated MBW complex then orchestrates the coordinated expression of the whole anthocyanin biosynthetic pathway.

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Table 3: Genes and Their Functions in Plant Cold Stress Response and Adaptation.

Gene	Crops	Role in Stress Response	Reference
DREB1/CBF, DREB2	Arabidopsis thaliana	Transcription factors regulating ABA-independent pathways; DREB1/CBF responds to cold, DREB2 to heat stress.	[9]
ICE1, ZAT12, CAMTA3, MYB15	Arabidopsis thaliana	Regulators of the DREB1/CBF pathway enhance cold tolerance.	[10]
C4H, F3H, DFR, ANS, UFGT	Brassica rapa, Arabidopsis thaliana	Anthocyanin biosynthetic genes; upregulated under low temperature to enhance pigment accumulation and cold tolerance.	[11]
BrANS1–BrANS3, BrDFR1–BrDFR10	Brassica rapa	Flavonoid biosynthesis genes show strong cold and freezing stress responses.	[8]
BZR1	Arabidopsis thaliana	Brassinosteroid signaling TF promotes CBF1/CBF2 expression and enhancing low-temperature resistance.	[13]
miR156 / SPL3	Arabidopsis thaliana	miR156 delays flowering at low temperatures by suppressing SPL3 expression.	[17]
MADS-box family	Brassica oleracea, Arabidopsis thaliana	Regulate floral organ development and cold-induced flowering transition.	[18 ; 19]
GSTs (Tau, Phi, DHAR, JrGSTU1)	Cucumis melo, Juglans regia	Glutathione S-transferase family involved in ROS detoxification and cold tolerance.	[22]
HD-ZIP family	Brassica rapa	Regulate cell membrane stability and ROS scavenging under cold stress.	[26]
BrLEA73 (LEA_6)	Brassica rapa	Late embryogenesis abundant protein enhancing low-temperature tolerance via ABA-related pathway.	[49]
BrSRO1–BrSRO9	Brassica rapa	Stress-responsive genes upregulated under cold, salt, and drought; regulate redox homeostasis.	[43]
GLYI, GLYII	Brassica juncea, Oryza sativa	Glyoxalase system genes induced by cold and heavy metal stress detoxify methylglyoxal.	[46]
COR genes	Nicotiana tabacum, Arabidopsis thaliana	Cold-regulated genes enhancing freezing tolerance.	[38]
SNAT / BcSNAT1	Brassica campestris	Serotonin N-acetyltransferase; involved in melatonin biosynthesis and stress signaling under cold.	[58]
AtHAP5A / AtXTH21	Arabidopsis thaliana	CCAAT-binding TF regulating freezing stress tolerance and ABA signaling.	[61]
GAox	Arabidopsis thaliana, Brassica spp.	Gibberellin oxidase family involved GA metabolism, growth, and stress response.	[62]
BcSOC1, BcLFY, BcEXPA11, BcXTH3, BcRGL1	Brassica campestris var. utilis	GA-responsive and cell wall genes controlling bolting and flowering under cold or GA_3 treatment.	[72 ; 73]
BrBASS7	Brassica rapa	Low-temperature responsive transporter gene containing ABA and auxin response elements.	[65]
BoTT8, BoMYB2 / BoPAP1	Brassica oleracea var. sabellica	Transcription factors regulating anthocyanin accumulation under cold stress.	[11]
BrPur	Brassica rapa	Controls purple leaf pigmentation; anthocyanin accumulation under cold stress.	[68]
Wax biosynthesis genes (e.g., CER, WAX, LTPs)	Brassica oleracea	Involved in cuticular wax biosynthesis and stress protection; mutations cause glossy phenotype.	[75]
nsLTPs	Brassica spp., Arabidopsis thaliana	Nonspecific lipid transfer proteins involved in cold, heat, drought, and salt stress.	[50]
ABA 8’-hydroxylase (S3)	Brassica rapa	Enzyme regulating ABA catabolism during abiotic stress response.	[56]
CBF–ICE–COR pathway	Arabidopsis thaliana, Brassica spp.	Central cold signaling cascade activating cold-responsive genes for acclimation.	[59; 60]
Brassicaceae glucosinolate (GSL) genes	Brassica rapa	Involved in secondary metabolite biosynthesis; modulated by cold and vernalization.	[25]
Circadian clock-related genes	Brassica rapa	Coordinate cold stress response and rhythmic gene expression.	[42]

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The key structural genes that code for early enzymes, including BrCHS and BrF3H, and later specifically dedicated genes, including BrDFR, BrANS, and BrUFGT, are all highly upregulated during chilling stress. Further, multiple (e.g., BrDFR1-BrDFR10 and BrANS1-BrANS3) cold-responsive paralogs of critical DFR and ANS have been reported in the B. rapa genome. This transcriptional cascade results in the biosynthesis and accumulation of anthocyanins, which serve as potent antioxidants to scavenge reactive oxygen species and as light-attenuating pigments to reduce photo-oxidative damage and enhance freezing and chilling tolerance (Ahmed et al., 2015). Moreover, hormone signaling interacts with this pathway, for which evidence has been provided by the ABA receptor gene BoPYL8, whose cold-induced expression and activity further promotes anthocyanin biosynthesis and cold acclimation in cabbage [69].

Flowering Chinese cabbage (Brassica campestris L. ssp. Chinensis var. utilis Tsen et Lee) is a highly cultivated and productive vegetable in southern China [70]. It belongs to the Chinese cabbage subspecies of Brassica species in the Brassicaceae family. The main product organ is the flowering stalk. The formation of the flowering stalk involves two simultaneous processes: bolting, which is characterized by stem elongation and thickening, and flowering. Gibberellin (GA) is a crucial factor influencing bolting in flowering Chinese cabbage. Treatment with exogenous gibberellin A3 (GA3) has been shown to induce the up regulation of BcSOC1 and genes encoding cell wall structural proteins (BcEXPA11, BcXTH3) in flowering Chinese cabbage, thereby facilitating early bolting and flowering processes. Moreover, low temperatures trigger GA accumulation at the stem tip, accelerating growth and flowering. Conversely, using a GA synthesis inhibitor (PAC) suppresses the initiation of bolting and flowering [71].

Loss-of-function mutations in BcRGL1, a DELLA protein, affect the expression of various genes in flowering Chinese cabbage. These genes include the GA regulatory gene BcGASA6, flower-related genes BcSOC1 and BcLFY, and genes encoding cell wall structural proteins BcEXPA11 and BraXTH3. These mutations promote flowering and bolting. Conversely, overexpression of BcRGL1 suppressed both bolting and flowering in flowering Chinese cabbage [72]. The proportion of aldehyde, primary alcohol, and ester significantly increases in leaf cuticle wax in Brassica oleracea var. gemmifera under lower light and higher temperature conditions, whereas the biosynthesis of alkanes, secondary alcohol, and ketones is enhanced at higher light and lower temperature levels [73]. The accumulation of glaucous powdery wax on the surface of leaves and stems is completely or partially dampened in wax-deficient mutants, so that wax-deficient leaves and stems generally exhibit a glossy green appearance. In cabbage, numerous wax biosynthesis-related genes have been characterized as glossy green mutants. A large number of genetic analyses have shown that most wax-deficient mutations in cabbage are controlled by a single recessive gene [74].

Conclusion

Cold stress represents a major constraint to the growth, development, and productivity of Brassica crops. Understanding the interplay among phytohormones, transcription factors, secondary metabolism, and circadian regulation provide valuable insights for breeding cold-tolerant cultivars with improved yield and nutritional quality.

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