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Horticultural Plant Cold Resistance Mechanism under WRKY Transcription Factor and Sugar Interaction

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Abstract Cold stress seriously affects the growth development of plants and crop yield. In order to ensure survival, plants have formed a complex and efficient regulatory network to resist the cold stress or gradually adapt to it. WRKY transcription factors play an important role in plant abiotic stress response. Although exogenous sugar can also improve the resistance of plants to cold stress, the response mechanism of plants to cold stress under the interaction between transcription factors and sugar is still unclear. In this review, the author introduced the damage of cold stress on plants, briefly summarized the mechanism and regulatory network of WRKY transcription factors in response to stress. Moreover, the author also reviewed the response of horticultural plants to cold stress after exogenous sugar and explained the possible cold resistance mechanism of horticultural plants under the interaction between WRKY and sugar, which aimed to provide some reference for the study of the internal molecular mechanism of horticultural plants coping with cold stress.

Keywords Horticultural plants; Cold stress; Exogenous sugars; WRKY transcription factor; Cold tolerance mechanism

Plants will suffer from cold injury or frostbite in cold environment. In order to ensure their survival, plants have developed many effective molecular mechanisms to protect cell activity and plant integrity during their long evolutionary process, among which transcriptional regulation is a common and very important molecular mechanism to cope with cold stress (Cheng et al., 2021).

Transcription factors (TFs) play an important role in plant growth and development. The WRKY TFs family is one of ten unique transcription factor families in plants, whose members are involved not only in the regulation of plant hormone signaling pathways, but also in abiotic stress signal transduction pathways, inducing the expression of many stress-related genes, thereby improving plant resistance to abiotic stress (Ran et al., 2014). In low temperature environment, the content of soluble sugars in plant cells increases due to the hydrolysis of some macromolecules, which can act as signaling molecules to regulate plant source-pool relationship and gene expression (Chen et al., 2002, Chinese Journal of Cell Biology, 24(5): 266-270; Pan et al., 2022). In addition, it was found that exogenous application of polysaccharides, disaccharides or monosaccharides could stimulate plant responses to cold stress to a certain extent, which could not be separated from the regulatory role of transcription factors in related signaling pathways.

In recent years, great breakthroughs and progress have been made in model plants such as rice (*Oryza sativa*) and Arabidopsis (*Arabidopsis thaliana*) (Cheng et al., 2021) in studying the molecular mechanisms of how plants sense, transmit and regulate low temperature signals. As an important signaling molecule in the cold signaling pathway, sugar has also attracted much attention. The study of Maruyama et al. (2009) showed that the accumulation of carbohydrate was related to the function of some cold resistance genes. In *Arabidopsis thaliana* overexpressing *DREB1A*, it was found that *DREB1A* and *DREB2A* could induce the expression of different carbohydrate metabolism genes in the downstream signaling pathway, promote the accumulation of various carbohydrate substances, and thus enhance the cold resistance of plants. However, it is not clear how plants improve their resistance to cold stress through transcriptional regulation and exogenous sugars. In this review, the changes of plant appearance and phenotype, different physiological and biochemical response mechanisms and molecular regulatory networks under cold stress were summarized, and the possible signaling pathways and cold resistance mechanisms of horticultural plants under the interaction of WRKY and sugar were discussed, providing references for genetic improvement of cold resistance of horticultural plants.

1 The Harm of Cold Stress to Plants

In the natural environment, plants are often exposed to adverse conditions, such as drought, cold, high salinity and heavy metals, which are collectively referred to as abiotic stress, and one of the most prominent stresses on plants is cold stress (i.e., low temperature stress) (Huang et al., 2022). It determines the geographical distribution of plants, growth and development, crop yield and fruit quality (Jeon and Kim, 2013). Many food crops and garden plants, such as corn (*Zea mays* L.), sorghum (*Sorghum bicolor*), rice (*Oryza sativa* L.), tomato (*Solanum lycopersicum*) and cucumber (*Cucumis sativus* L.), will be adversely affected by cold stress. According to relevant statistics, the global economic losses caused by low temperature damage in agriculture are as high as hundreds of millions of yuan every year, which will reduce the average yield of crops by 13% to 15%. In China, cold stress occurs frequently in early spring and late autumn, leading to a series of reactions such as freezing of plant cell membranes, which directly or indirectly inhibit plant growth and cause irreversible damage (Thakur and Nayyar, 2013; Song et al., 2019; Pan et al., 2021). Therefore, it is of great significance to explore the mechanism of plant cold resistance and how to improve plant cold resistance.

1.1 Changes of plant appearance and phenotype under cold stress

Cold stress has great influence on plant appearance and phenotype. The expression of chilling injury is very flexible, and different plant parts show different susceptibility. The direct manifestations of plants under cold stress include leaf curl and wilting, stem cracking, tissue discoloration, water soaking leaves, immature fruit, reduced quality, local tissue necrosis, root rot, loss of regenerative vitality, etc. (Sharma et al., 2020) (Figure 1). In addition, cold damage can also cause seedling weakness, fruit blotching, plant growth retardation, yellowing, low fruit setting rate, decreased yield and leaf lesions, etc. Among different cold-sensitive plants, the most affected plant parts are leaves, fruits and flowers, and the most common manifestation is the wilting of leaves with purple or red color (Wu et al., 2015; Mukhopadhyay and Roychoudhury, 2018).

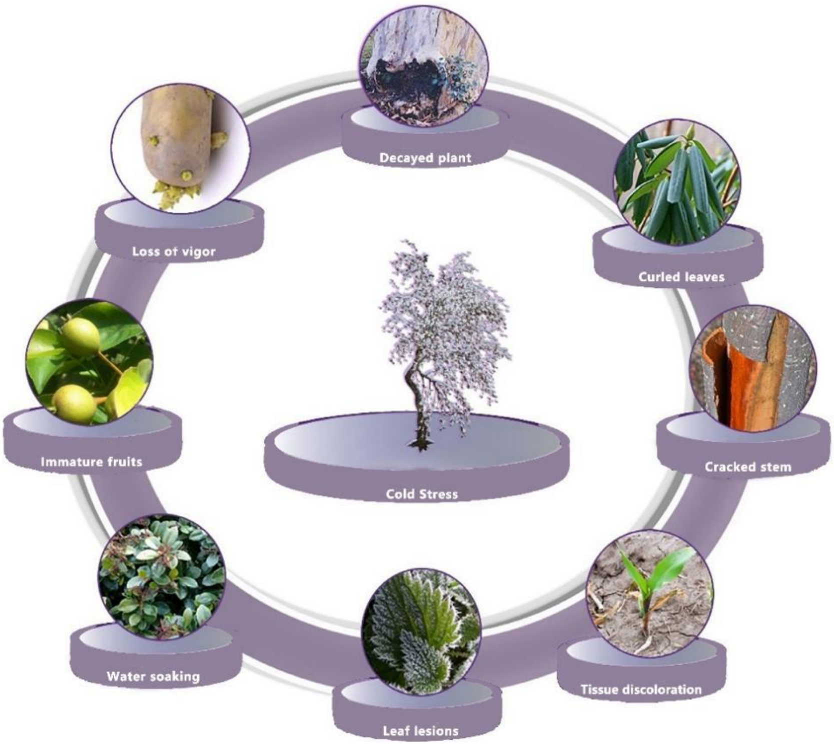

Figure 1 Effects of cold stress on the plant phenotype (Sharma et al., 2020)

1.2 Changes in plant physiology and biochemistry under cold stress

The cell membrane serves as the first line of defense against cold stress and is the most directly affected site by low temperatures (Ding et al., 2019). Low-temperature stress can lead to lipid peroxidation of plant cell membranes. Simultaneously, it alters the membrane's permeability, increasing its relative permeability, which causes solute leakage from the cells. This disrupts intracellular ion balance, further affecting enzyme activity, subsequently resulting in metabolic disturbances in plants. Toxic substances accumulate within the plant because they cannot be efficiently expelled (Song et al., 2019). These series of changes disrupt the plant's original homeostasis, affecting its growth and development and, in severe cases, causing irreversible damage that ultimately threatens the plant's survival (Theocharis et al., 2012).

When plants are exposed to cold environments, such as sudden temperature drops or occurrences of "late spring coldness", they initiate self-protective mechanisms to adapt to the conditions. By activating specific transcriptional programs, they strike a new balance between development and defense against stressful environments (Zhang et al., 2020). Initially, changes occur in plant cell membrane structure, membrane fluidity, and metabolites. Additionally, there is an increase in calcium content in plant cellsap, alterations in nucleotide conformations, and changes in protein conformations. These changes activate transcription factors within the plant. Under the regulation of these transcription factors, second messengers, abscisic acid, and reactive oxygen species undergo corresponding alterations. These collective changes constitute the cold stress signals, activating the expression of specific genes within the plant to adapt to and defend against cold stress (Sharma et al., 2020). Consequently, plants undergo a series of physiological and biochemical changes following exposure to cold stress (Figure 2).

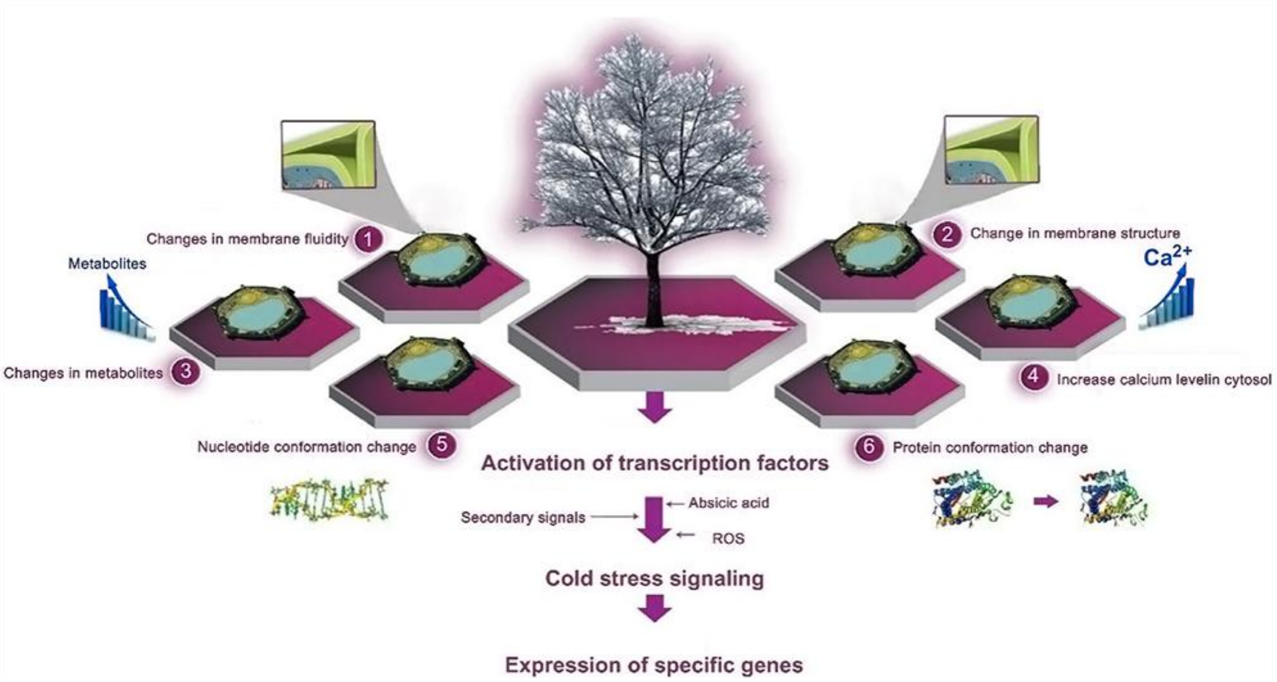

Figure 2 A series of responses produced by plants under cold stress (Sharma et al., 2020)

1.3 Changes in plant molecular mechanisms under cold stress

Plants employ various complex mechanisms to adapt to cold stress, allowing them to rapidly perceive and transduce stress signals and initiate cold tolerance responses to protect themselves from cold damage. This process involves intricate physiological and gene expression regulatory networks. When plant cell membranes feel cold stress, calcium ions, as crucial second messengers in cold signal transduction, work in conjunction with other second messengers like abscisic acid to transmit stress signals downstream (Zhang et al., 2009). Calcium-binding proteins known as calcium sensors play a primary role in this process by increasing cytoplasmic calcium ion concentration, thereby altering the phosphorylation status of various proteins (Wang et al., 2020).

Since temperature is a physical signal, all organelles within plant cells can directly or indirectly sense temperature changes (Zhu, 2016). Once these physical signals are sensed by various organelles, they must be decoded by downstream macromolecules to regulate gene expression and other cellular activities. Cold stress induces osmotic stress in plant cells, triggering a rapid and transient increase in cytosolic solute [Ca^{2+}]([Ca^{2+}]$_{cyt}$). Calcium ions serve as universal second messengers and initiate responses to abiotic stress by activating specific Ca^{2+} permeable channels and Ca^{2+} transport proteins (Gong et al., 2020). Plants possess a multitude of calcium channels and transporter families such as glutamate receptor channels (GLRs), cyclic nucleotide-gated channels (CNGCs), and calcium-permeable transport membrane proteins, which coordinate specific cytosolic calcium ion signals in plants under stress (Chen et al., 2021). Studies have found that OsCNGC9 (Wang et al., 2021) and calcium transporter membrane protein 1 (AtANN1) (Liu et al., 2021) mediate cold-induced calcium influx in rice and Arabidopsis, respectively (Figure 3). Further research is needed to understand how these calcium ion channels and transporters are regulated to produce specific calcium ion signals in response to cold stress. Additionally, literature suggests that the MAPK family acts upstream of the WRKY family (Jia et al., 2020), many WRKY transcription factors participate in MAPK cascade reactions (Zhang et al., 2008), and they regulate plant defense responses through interactions between WRKY and MAPK (Chi et al., 2013).

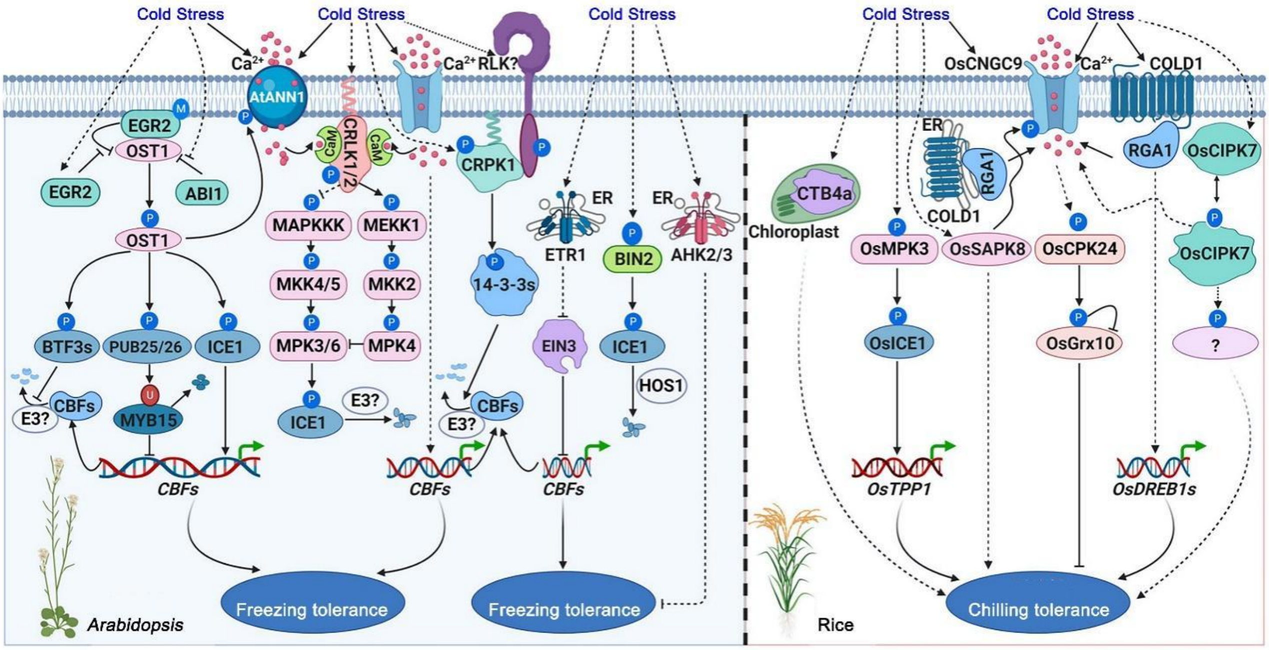

Figure 3 Cold signal transduction mediated by protein kinases in Arabidopsis and rice (Chen et al., 2021)

2 The Role of WRKY Transcription Factors in Horticultural Plant Responses to Cold Stress

WRKY transcription factors contain at least one DNA-binding WRKY domain, and WRKY proteins regulate the expression of target genes by binding to the W-box in the promoter region (Liu et al., 2014). The first member of the WRKY TFs was discovered in sweet potato (*Ipomoea batatas*) and was named SPF1 (Bi et al., 2021). Previous research has demonstrated the significant role of WRKY TFs in stress responses. They not only regulate the growth and development of crops but also participate in various physiological activities such as sugar synthesis, organ development, aging, and resistance to various stressors in plants (Chen et al., 2022). In response to cold stress, the involvement of WRKY TFs has been identified in many horticultural plants (Table 1), and with the advancement of bioinformatics, numerous WRKY gene families have been identified and characterized (Yang et al., 2020).

Table 1 WRKY transcription factors in partial response to low temperature

Gene name	Species name	Research method	Reference
PheWRKY1-1 *PheWRKY50-1*	*Phyllostachys edulis*	Transcriptome analysis	(Huang et al., 2022)
SmWRKY26 *SmWRKY32*	*Solanum melongena*	Transcriptome analysis	(Yang et al., 2020)
CsWRKY46	*Cucumis sativus*	Overexpression into *Arabidopsis*	(Zhang et al., 2016)
PmWRKY57 *PmWRKY40*	*Armeniaca mume*	Transcriptome analysis	(Peng et al., 2019; Wang, 2021)
VaWRKY33	*Vitis amurensis* Rupr.	Overexpression into *Arabidopsis*	(Sun et al., 2019)
TaWRKY93	*Triticum aestivum*	Transcriptome analysis	(Qin et al., 2015)
MaWRKY31 *MaWRKY33* *MaWRKY60* *MaWRKY71*	*Musa nana* Lour.	Transcriptome analysis	(Luo et al., 2017)
BnWRKY	*Brassica napus*	Transcriptome analysis	(Du et al., 2021)
CmWRKYs	*Cucumis melo* L.	Transcriptome analysis	(Zhang and Wei, 2020)
AtWRKY34	*Arabidopsis thaliana*	Overexpression into *Arabidopsis*	(Zou et al., 2010)
OsWRKY71	*Oryza sativa*	Northern blotting	(Kim et al., 2016)
VbWRKY32	*Verbena officinalis* L.	Transcriptome analysis	(Wang et al., 2020)
SlWRKY12 *SlWRKY13* *SlWRKY23* *SlWRKY50* *SlWRKY51*	*Solanum lycopersicum* L.	Collinearity analysis	(Chen et al., 2015)

2.1 Mechanisms of WRKY response to stress

In studies of plant responses to stress, it has been demonstrated that WRKY transcription factors can mediate plant responses to various stressors by regulating pathways such as plant hormone signal transduction. They can interact with and play regulatory and balancing roles in signaling pathways involving signaling molecules like abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) (Ren et al., 2021; Chen et al., 2022). Wang et al. (2020) found that the expression level of the cotton (*Gossypium* spp) transcription factor *GhWRKY21* can be induced by abiotic stresses like drought and low temperature, and it is induced by signaling molecules like ABA. Yeast one-hybrid experiments showed that *GhWRKY21* can directly bind to the W-box in the promoter of GhHAB, negatively regulating ABA-mediated drought resistance through the modulation of GhHAB expression. WRKY TFs are key nodes in the ABA response signaling network. To cope with stress encountered during growth, plants can alter their gene expression patterns and metabolic pathways, reprogramming their transcriptomes to adapt to adversity. WRKY transcription factors participate in the regulatory networks of various stresses in plants, acting as either activators or repressors (Bai et al., 2018) (Figure 4).

2.2 WRKY-mediated regulatory networks in response to cold stress in horticultural plants

WRKY transcription factors, as key switches in signal networks, serve as excellent targets for studying the molecular mechanisms of signal responses. Plant responses to cold stress are associated with a complex and precise process of transcriptional reprogramming. Deciphering the transmission mechanisms of cold signals in plants can reduce the damage caused by cold stress, and the involvement of *WRKY* genes in the response to cold stress has demonstrated their role in regulating plant cold resistance. Preliminary evidence suggests that *SmWRKY26* and *SmWRKY32* positively regulate eggplant's cold tolerance through virus-induced gene silencing (VIGS) (Yang et al., 2020). In the model plant rice, *OsWRKY71* enhances its cold tolerance by regulating the expression of downstream genes *OsTGFR* and *WSI76* (Kim et al., 2016). OsMADS57 directly acts on the *OsWRKY94* gene and induces its expression in a temperature-dependent manner. Under normal growth conditions, *OsWRKY94* gene expression is suppressed, but after rice undergoes cold stress, the expression of the *OsWRKY94* gene is activated. Therefore, the *OsWRKY94* gene participates in the regulation of the rice cold signaling pathway and acts as a positive regulator of cold resistance (Chen et al., 2018). Cells rapidly receive cold signals after cold stress, and these signals undergo complex signal transduction before ultimately reaching the regulatory sites to respond to environmental stress. The interactions between the cold signaling pathway, TFs that regulate cold stress, and cold-induced genes significantly control horticultural plant responses to cold stress, highlighting the complexity of cold regulation (Liu et al., 2014) (Figure 5).

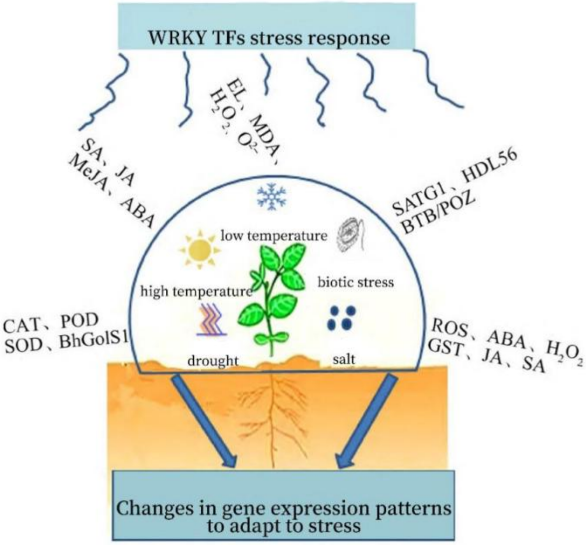

Figure 4 Proposed model of WRKY TFs responses under stresses conditions (Chen et al., 2022)

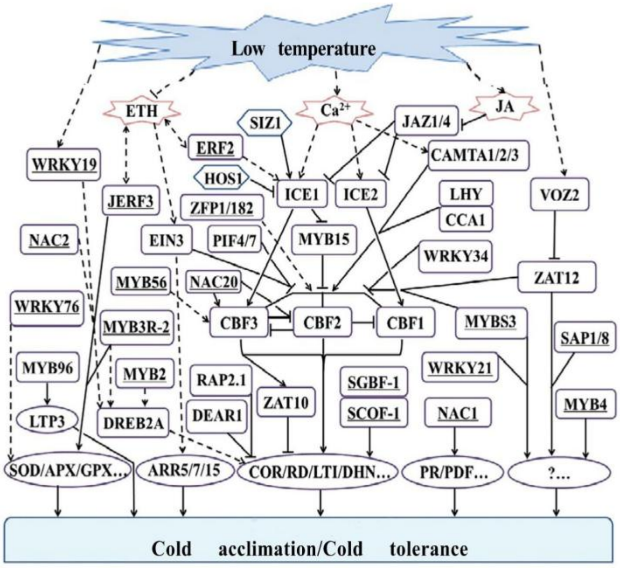

Figure 5 Diagram of cold-responsive transcriptional regulation network in plant (Liu et al., 2014)

3 Exogenous Sugar Regulation in Horticultural Plants

3.1 Regulation of exogenous sugars on horticultural plant growth and development

Sugars serve as the fundamental substances underlying the growth and development of plant fruits. Among these sugars, monosaccharides like fructose and glucose, as well as disaccharides like sucrose, are the three primary forms, and the quality of fruit is largely influenced by the content and ratio of these three sugars. Research by Ling et al. (2018) demonstrated that the exogenous application of sucrose significantly increased both the individual fruit weight and sweetness of strawberries (*Fragaria* × *ananassa* Duch.). Moreover, treating ripe strawberries with a 100 mmol/L sucrose solution yielded the best results, greatly increasing the content of their major bioactive substances. Peng et al. (2020, Journal of Green Science and Technology, (17): 82-84) found that a certain concentration range of sucrose treatment significantly increased the soluble sugar content during the development of blueberries (*Vaccinium* spp.), enhancing fruit quality. The best results were obtained when blueberries were treated with a 1% sucrose solution.

3.2 The related ways of exogenous sugars improving cold resistance of horticultural plants

Soluble sugars are the primary substances for organic material transport and storage in both "source" and "sink" tissues. Sugars in plants not only participate in cellular metabolism but also promote plant growth, development, and responses to environmental stressors (Wang et al., 2020). When plants face cold environmental conditions, changes in cell osmotic potential occur due to increased sugar levels resulting from low-temperature stress. Plants accumulate soluble sugars and other small molecules to maintain intracellular water balance and membrane stability. Osmotic potential and water potential of cells are dynamically regulated to prevent cytoplasmic dehydration, thereby avoiding cold-induced cytoplasmic gelation, ultimately enhancing plant cold resistance (He et al., 2016; Verma et al., 2011). Additionally, sugars can serve as signaling molecules in the regulation of plant cold resistance. A highly effective approach to alleviate the damage caused by abiotic stress to plants is the application of exogenous sugars. Previous research has shown that the application of exogenous sugars can effectively enhance the resistance of horticultural plants to cold stress. Huang et al. (2021) used chitosan to treat melon (*Cucumis melo* L.) seedlings under low-temperature stress through seed soaking, foliar spraying, and root irrigation. The study found that all three treatments effectively alleviated the damage to melon seedlings under low-temperature stress, improving the quality and cold tolerance of melon seedlings and promoting plant and root growth. This suggests that the exogenous application of chitosan can further increase the content of osmotic regulation substances in melon seedlings, helping to maintain their osmotic balance and membrane stability, thereby enhancing the cold resistance of horticultural plants (Wei et al., 2021).

Soluble sugars have a dual role in reactive oxygen species (ROS) as both prooxidants and antioxidants. They can participate in the pathways for ROS and NADPH production, such as the pentose phosphate pathway (OPP), thus enhancing ROS clearance efficiency to some extent (He et al., 2016). Research has shown that chitosan enhances the cold resistance of wheat (Wang et al., 2016). In the sugar signaling pathway, sucrose (SUC) acts as a signaling molecule in the regulation of plant growth and development, and its signal system can induce and activate the antioxidant system within plants. Diao et al. (2020) found that a certain concentration of SUC can increase the activity of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) in melon seedlings under low-temperature stress, reducing cold stress damage.

3.3 Enhancement of cold resistance in horticultural plants by exogenous sugar response

Under low-temperature stress, plants stimulate sugar production through a series of reactions to respond to cold stress. Increasingly, research indicates that cold acclimation affects sugar metabolism, reflecting the important role that sugar plays in plant cold resistance. Diao et al. (2019) found that low-temperature stress increased the activity of nitric oxide synthase in melons to stimulate NO synthesis. This, in turn, promoted the activity of enzymes related to sucrose metabolism, increasing the soluble sugar content in response to low-temperature stress. Pan et al. (2021) discovered that exogenous trehalose can jointly regulate the response of rice variety ‘Yu17S’ to low-temperature stress with the H_2O_2 signaling molecule, thereby enhancing its cold resistance. Wei et al. (2021) found that in the late growth and development of grapevine stems, the relationship between sugar content in the phloem and cold resistance is more closely related. Therefore, an increase in sugar content can be one of the mechanisms for improving grape cold resistance.

It has been confirmed that there are two major signal transduction pathways in plants in response to low-temperature stress: ABA-dependent and ABA-independent pathways. Hence, ABA can participate in cold resistance regulation. Endogenous ABA levels vary significantly among varieties with different cold resistance. Xiang et al. (2019) showed that under cold stress, ABA content in plants exhibited a clear upward trend and was positively correlated with cold resistance. In different varieties, the higher the ABA content, the stronger their cold resistance (Wei et al., 2021). Sugars can regulate hormone signals at the transcriptional level. The core mechanism of glucose signal transduction pathway is the induction of ABA and ABI gene expression. Genes like *ABI4*, *ABI5*, and *CTR1* involved in the sugar signal pathway are specifically regulated by glucose, ABA, stress, and developmental stages (Rolland et al., 2006). In the plant sugar signal pathway, hexokinase (HXK) can act as a sensor for sucrose and glucose, perceiving sugar signals between cells, thereby regulating the transcriptional expression of relevant genes, triggering sugar signal transduction. Additionally, HXK1 can regulate the expression of transcription factors like WRKY in the plant cell nucleus, allowing them to play a role in the joint regulation of plant stress responses (Figure 6). However, the specific regulatory mechanism is not yet clear (Lei et al., 2007).

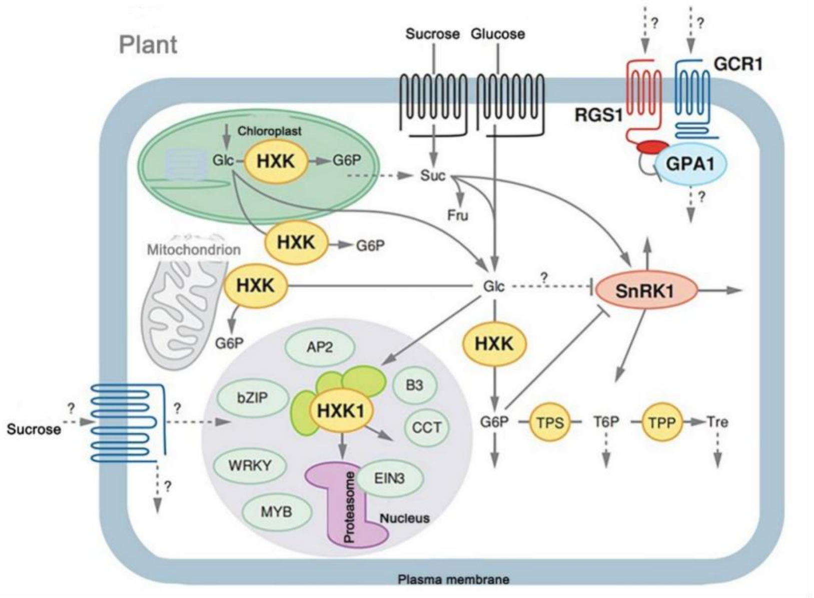

Figure 6 Model of sugar-sensing mechanisms in plants (Rolland et al., 2006)

Genes associated with the sugar signaling pathway in plants either positively or negatively regulate plant cold resistance. Zhang et al. (2017) and An et al. (2017) conducted a study on rice and found that the gene *OsTPP1* (Trehalose-6-phosphate phosphatase 1), involved in trehalose-6-phosphate dephosphorylation, prevents the upregulation of the ubiquitination degradation pathway (*OsMAPK3-OsbHLH002-OsTPP1*) mediated by RING E3 ligase OsHOS1 (High expression of osmotically responsive gene 1) under low-temperature conditions. This ultimately confers strong cold resistance to rice and enhances its survival rate under cold stress. Additionally, the transcription factor OsMADS57 interacts with OsTB1, regulating the balance between rice plant growth and cold resistance (Lü et al., 2017). OsMPK3 enhances low-temperature tolerance by increasing the accumulation of trehalose, and OsDREB1s also play a crucial role in promoting cold resistance in plants (Chen et al., 2022). In contrast, the transcription factor OsMYB30 interacts with OsJAZ9, inhibiting the expression of β-amylase, which leads to a reduction in the level of osmoprotectant maltose. Consequently, this negatively regulates plant tolerance to cold stress. When cold signals are sensed by the low-temperature receptor COLD1 and an unknown cold sensor, plant cold tolerance is enhanced through the production of hormones or osmoprotectants such as trehalose and maltose. OsbZIP71 forms a complex with OsbZIP73 to regulate ROS and ABA levels under low-temperature stress. Moreover, OsMPK3 enhances low-temperature tolerance by increasing trehalose accumulation, while OsMYB30 interacts with OsJAZ9 to inhibit maltose production in response to low-temperature stress (Chen et al., 2022).

4 WRKY Involvement in Regulating Cold Resistance in Horticultural Plants

Plants accumulate sugar substances as an important mechanism to withstand cold temperatures. Sugar metabolism is closely associated with a plant's response to low-temperature stress, and the content of soluble sugars directly impacts a plant's cold resistance (Yang et al., 2020; Yu et al., 2021, Journal of Tea Communication, 48(4): 652-662). Within the sugar signaling pathway, transcription factors like WRKY participate in regulating the expression of cold stress-related genes, thus enhancing cold resistance in horticultural plants. The WRKY transcription factor SPF1, originally identified in sweet potatoes, was among the first involved in regulating sugar metabolism pathways and potentially influencing sucrose biosynthesis (Ishiguro and Nakamura, 1994). A more in-depth study by Bi et al. (2021) using bioinformatics methods on sweet potatoes revealed that the protein sequence of SPF1 shared a high degree of similarity with IbWRKY32, with a sequence identity of up to 85.4%, and the WRKY conserved domains were entirely identical. This suggests that SPF1 and IbWRKY32 are highly homologous, implying that *SPF1* gene is functionally similar to the *IbWRKY* gene. Furthermore, *IbWRKY32* was upregulated in response to cold stress during the storage period of storage roots in two sweet potato varieties with different cold tolerance. This indicates that *IbWRKY32* plays a role in enhancing sweet potato storage root cold resistance, suggesting its involvement in regulating sweet potato's tolerance to cold stress by participating in the sucrose signaling pathway. The *BhWRKY1* gene in *Boea hygrometrica* (Bge.)R.Br. can bind specifically to the W-box in the promoter of the myo-inositol galactoside synthase *Gol S* (Galactinol synthase) gene. *Gol S* catalyzes the first step in the biosynthesis of raffinose family oligosaccharides (RFOs), crucial osmoprotectants in horticultural plants' defense against cold stress (Luo et al., 2015, Chinese Journal of Tropical Crops, 36(3): 629-637).

WRKY transcription factors potentially act as a hub in the ABA signaling network, participating in the sugar signaling pathway to jointly enhance cold resistance. The core key genes in the ABA signaling network are *ABI4* and *ABI5*, which can also be involved in the sugar signaling pathway during stress conditions (Sun et al., 2017). Research by Zhang et al. (2016) suggests that the *CsWRKY46* gene in cucumbers is a positive regulator of cold resistance, and it exhibits synergistic effects with ABA under low-temperature stress. They propose a model in which *CsWRKY46* mediates the cold stress regulatory pathway. Cold stress induces *CsWRKY46* activity, activating *ABI5* through an ABA-dependent pathway, subsequently upregulating the expression of stress response genes and functional genes, thereby enhancing cold resistance. The *BcWRKY46* gene in rapeseed, when overexpressed in transgenic tobacco, increases its tolerance to low temperatures while reducing its sensitivity to ABA. This suggests that the *BcWRKY46* gene can activate relevant genes in the ABA signaling pathway, thereby enhancing cold resistance in horticultural plants (Wang et al., 2012; Wang et al., 2014).

WRKY transcription factors are likely involved in regulating the biosynthesis and metabolism of non-structural carbohydrates like sucrose (Li et al., 2018; Huang et al., 2019). For instance, the expression of *VvWRKY22* is inhibited by exogenous sucrose but induced by fructose, indicating its role in regulating sugar metabolism (Huang et al., 2021b). *OsWRKY11* in rice activates the expression of raffinose synthesis-related genes, thereby increasing the content of raffinose in plants (Wu et al., 2009; Wang et al., 2014). Huang et al. (2021a) discovered that *VvWRKYs* respond to both sugar and ABA. Co-expression network analysis indicated that *VvWRKYs*, sugar, and ABA-related genes appear to be interconnected, suggesting potential functions of *VvWRKYs* in regulating sugar and ABA signaling pathways during grapevine growth and development.

WRKY transcription factors may be involved in regulating cold resistance in horticultural plants through sugar transport proteins (SUC). Sugar transport proteins play a crucial role in responding to environmental stressors, which is closely linked to a plant's resistance (Li et al., 2018). Yuan et al. (2014) conducted PLACE analysis of the SUC gene family in the AC genome of *Brassica* genus, revealing that all *SUC* genes have multiple WRKY elements in their promoter regions, which are associated with stress responses. This suggests that *SUC* genes participate in stress responses. Research indicates that the *OsWRKY71* gene in rice plays a positive regulatory role during cold acclimation (Kim et al., 2016). WRKY transcription factors are also involved in the response to sugar starvation. In sugar-starved rice suspension cells, *OsWRKY72* plays a role in sugar and ABA signal crosstalk (Wang et al., 2007). Overexpressing *OsWRKY72* in Arabidopsis significantly increases its sensitivity to ABA and sugar starvation (Song et al., 2010). *HvWRKY46* regulates the sugar signaling pathway by modulating the expression of *ISO1* and *SBEllb* (Sun et al., 2007). *AtWRKY4* and *AtWRKY34* play a regulatory role in the induction of AtNDPK3a by sucrose and glucose (Hammargren et al., 2008).

Research has shown that WRKY transcription factors interact with VQ proteins to coordinate horticultural plant responses to various abiotic stresses. VQ15 interacts with WRKY25 and WRKY51, playing a role in osmotic stress responses (Cheng et al., 2012). The interaction between MaVQ5 and MaWRKY26 weakens MaWRKY26's activation effect on JA synthesis genes, thereby regulating banana's response to cold stress (Hu et al., 2013). However, the precise interactions between WRKY transcription factors and VQ proteins under specific physiological conditions are still largely unknown. Investigating the relationship between WRKY transcription factors and VQ proteins is crucial for understanding the biological roles of VQ proteins. The continuous discovery of WRKY interacting proteins will provide a more solid theoretical foundation for unraveling the complex regulatory networks involving WRKY proteins (Cai et al., 2019, Journal of Anhui Agricultural University, 46(6): 1040-1047). It is predicted that WRKY-VQ complexes may participate in the regulation of sugar signaling pathways under cold stress.

In summary, cold stress activates the expression of WRKY transcription factors that contribute to cold resistance in horticultural plants (Zhang et al., 2016). Some WRKY transcription factors are involved in the response to sugar starvation or participate in sugar metabolism signaling pathways by regulating related gene expression (Song et al., 2010; Ran et al., 2014). Soluble sugars play a positive regulatory role in horticultural plant cold acclimation (Liang et al., 2022), and cold stress promotes the accumulation of soluble sugars in horticultural plants (Xu and Yu, 2022). Therefore, there may be a synergistic regulatory relationship between cold stress, WRKY transcription factors, and sugars. The key components and regulatory networks within this relationship require further in-depth exploration (Figure 7).

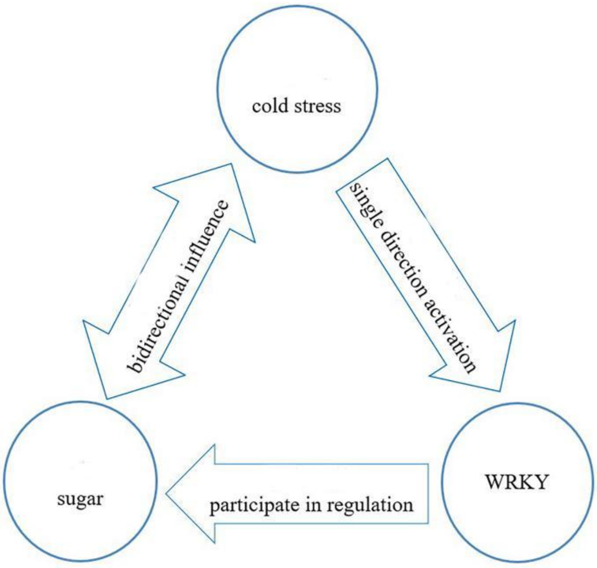

Figure 7 A putative model of the relationship among cold stress, WRKY and sugar

5 Summary and Progress

In response to cold stress, plants have developed complex molecular regulatory mechanisms that exhibit both similarities and differences across different plant species. WRKY transcription factors play roles in the cold signaling pathway, sugar signaling pathway, and ABA signaling pathway. There is interaction between the ABA and sugar signaling pathways, and WRKY transcription factors may act as a central hub via the ABA signaling pathway to participate in the sugar signaling pathway, thereby jointly regulating the cold resistance of horticultural plants. This review provides an overview of the associations between the signaling pathways in horticultural plants responding to cold stress and the potential mechanisms by which WRKY acts as a central transcription factor in jointly regulating cold resistance in horticultural plants. However, the detailed processes of cold resistance in horticultural plants and the coordination between cold signaling pathways and sugar signaling pathways remain unclear. The cold resistance of horticultural plants depends on the signal transduction of a series of factors within their cells. Plants can perceive cold stress signals at different levels and transmit them step by step, activating transcription factors that respond to cold stress, inducing the expression of various functional genes during stress resistance, initiating cold stress defense mechanisms, and forming a regulatory network for stress response. This deepens our understanding of the signal transduction of cold stress in horticultural plants.

Identifying key transcription factors and determining their central roles is important for understanding the relationship between cold signaling pathways and sugar signaling pathways. It also helps uncover the mechanisms of their interaction and inspires insights into sugar accumulation in plants under low temperatures. This knowledge can provide ideas for enhancing the cold resistance of cold-sensitive horticultural plants through the application of sugars.

Currently, with the continuous deepening of research on WRKY transcription factors and sugar signaling pathways in horticultural plants under abiotic stress, the application of various omics technologies, and the development of genetic engineering techniques, the role of WRKY in signaling transduction and regulation networks, including sugars, will become increasingly enriched in horticultural plants. A comprehensive understanding of the life activities of horticultural plants under abiotic stress will be further deepened, ultimately providing new and effective avenues for improving the resistance of horticultural plants. Although the interaction between WRKY and sugars has been demonstrated in horticultural plants responding to cold stress, the mechanism by which exogenous sugars and WRKY jointly induce the expression of cold stress-related genes in horticultural plants is not yet known. Questions about which downstream target genes are regulated to maintain ion homeostasis and enhance stress resistance, as well as how WRKY and sugars cooperatively respond to cold stress and regulate the cold resistance of horticultural plants, remain unclear. In the future, bioinformatics can be used to further explore the relationship between WRKY transcription factor expression and sugar signaling transduction pathways under cold stress. The elucidation of the mechanism of interaction between WRKY and sugars will be one of the effective strategies for improving the resistance of horticultural crops.

Authors' contributions

SHL was the primary author of the review, responsible for collecting and analyzing relevant literature, as well as drafting the initial paper. SB and XH participated in the analysis and organization of literature. ZY was the proposer and leader of the project, directing paper writing. All authors read and approved the final manuscript.

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