Review

Investigate the physiological, biochemical, and productivity aspects of crops to cold stress

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Abstract

Cold stress is one of the environmental factors that affects the growth, development, and productivity of crops in various climates. Understanding the physiological and biochemical mechanisms by which plants respond to this stress can help improve their growth and development. Cold stress can be categorized into two types: freezing stress and chilling stress. Freezing stress occurs when the temperature drops below 0 °C, while chilling stress occurs when the temperature ranges between 0 and 15 °C. Cold stress leads to the destruction or alteration of membrane lipids and proteins, causing a loss of membrane fluidity. This stress also increases the production of reactive oxygen species (ROS), which attack and destroy cell membranes. If cold stress persists, it can ultimately result in plant death. The ICE1-CBF-COR transcription cascade serves as a major signaling pathway activated in response to cold stress in plants. This cascade involves the induction of CBF (C-repeat binding factor) genes, which encode transcription factors that bind to the promoter of cold-responsive (COR) genes, initiating their transcription. Enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and glutathione reductase (GR) exhibit increased activity in response to low temperatures. Additionally, the accumulation of malondialdehyde (MDA) can serve as an indicator of oxidative stress sensitivity and cold tolerance. Cold stress has detrimental effects on crop yield formation. It initially impairs the reproductive phase of plants, ultimately leading to reduced final yields.

Keywords: Cold, Chilling, Freezing, ICE1, COR Genes

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Introduction

Cold stress is considered the most significant environmental factor that affects plant growth, yield, and ultimately leads to significant crop damage (Ahmad et al., 2014). Plants can be damaged by sudden temperature changes, primarily due to severe water deficits (Thomashow, 1999). Low temperatures, typically ranging from 0 to 15 °C and referred to as chilling temperatures, can also disrupt the water and nutrient relationships within plants (Theocharis et al., 2012). These symptoms ultimately result in a notable decrease in both the quality and yield of plants (Hassan et al., 2021). The manifestation of cold-induced stress damage in cold-sensitive plants differs from cold-tolerant ones, occurring within 2 or 3 days of exposure to cold stress

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(Pareek et al., 2017). The impact of cold stress on plant species depends on the variety, duration, and intensity of the stress, as well as the developmental stage (Simova-Stoilova et al., 2008). Previous studies have indicated that cold stress can inhibit phloem transport (Strand et al., 1997), reduce carbon fixation (Hurry and Huner, 1992), disrupt the circadian rhythm by regulating the transcription of photosynthetic genes (Martino-Catt and Ort, 1992), and lead to the destruction of damaged photosystem II (PSII) reaction centers (Krupa et al., 1990). The geographical distribution of crops is affected by cold stress, which hinders their growth. Furthermore, cold stress severely limits the biochemical and physiological activities of plant cells. In the early seedling stage, cold stress can cause leaf chlorosis, followed by wilting and even necrosis as its intensity increases (Ruelland and Zachowski, 2010). Low temperatures cause various changes in the biochemical and physiological processes of plants (Farooq et al., 2017). The response to cold stress in plants involves the perception and transmission of signals through a transcriptional cascade consisting of various signal transduction components that result in changes in gene activity (Yousefi et al., 2022). Generally, physiological processes, including photosynthesis, are sensitive to low temperatures, resulting in reduced plant growth and performance. Oxidative stress occurs in cells due to excess electron leakage to O_2 during respiration and photosynthesis, leading to increased production of reactive oxygen species (ROS). These ROS can damage membrane proteins, DNA, and lipids, ultimately causing cell death (Simova-Stoilova et al., 2008). Under optimal conditions, there is a tightly controlled balance between ROS formation and its scavenging by the antioxidant defense system of the plant. Superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) are key antioxidants that play a crucial role in plant defense against reactive oxygen species (Simova-Stoilova et al., 2008; Noctor and Foyer, 1998). Plant hormones are small molecular weight compounds involved in regulating plant growth and development (Devireddy et al., 2021). Moreover, a variety of studies suggest that cold stress responses are mediated by plant hormones (Hu et al., 2016). Therefore, this research was conducted to investigate the physiological, biochemical, and productive aspects of crops under cold stress.

The role of phytohormones in gene regulation to cold tolerance

Cold stress significantly alters several physio-biochemical processes in plants. For instance, exposure to cold stress (4°C for 7 days) in wheat (*Triticum aestivum* L.) has been shown to decrease photosynthetic efficiency, transpiration, and stomatal conductance, while increasing levels of reactive oxygen species (ROS) and malondialdehyde (MDA). Consequently, these changes lead to a reduction in both root and shoot growth (Repkina et al., 2021). The photosynthetic apparatus is highly susceptible to the effects of cold stress, resulting in a decrease in photosynthetic activity and chlorophyll synthesis (Liu et al., 2019). To counteract the detrimental effects of low temperatures, plants employ defense mechanisms such as osmotic regulation and antioxidant enzymes. Osmotic adjustments facilitate the accumulation of compatible solutes (osmo-protectants), which help protect cell structure and maintain turgor pressure (Wang et al., 2019). This accumulation of osmolytes and antioxidants aids in enhancing the plants' tolerance to cold stress (Jan et al., 2018).

When exposed to low temperatures, plants exhibit various responses, including changes in cell membrane fluidity, disruption of protein structures, decreased activity of antioxidant enzymes, increased production of ROS, alterations in photosynthesis, damage to cell membranes, and electrolyte leakage. Additionally, cold stress influences gene expression patterns and protein synthesis (Ding et al., 2019). Superoxide dismutase (SOD) is the first line of defense against ROS. The inactivation of ROS is carried out by the SOD enzyme. The activity of this enzyme increases in cold-tolerant species and decreases in cold-sensitive chickpea species (Heidarvand and Maali-Amiri, 2013). Following exposure to low temperatures, there is an increasing trend in ascorbate peroxidase (APX), catalase (CAT), SOD, and glutathione reductase (GR) activity, along with proline accumulation in chickpea (*Cicer arietinum*

L.) and *Lygodium microphyllum* L. (Singh et al., 2017). The accumulation of MDA is higher in cold-sensitive rapeseed cultivars compared to tolerant cultivars (Yan et al., 2019). A similar trend has also been reported in spring canola. Lipid peroxidation occurs less in tolerant cultivars than in cold-sensitive cultivars, resulting in lower levels of MDA in tolerant cultivars. MDA serves as an important indicator for oxidative stress sensitivity analysis and is a reliable measure of plant cold tolerance in plant breeding (Moieni-Korbekandi et al., 2014). Nandagopal and Shanmugam (2022) observed that glutathione peroxidase (GPX) activity is correlated with CAT, and both enzyme activities significantly increase in all genotypes of pepper (*Capsicum annuum* L.) under cold stress conditions. At the molecular level, cold stress affects membrane fluidity and subsequently alters membrane permeability. Plants respond to cold stress by inducing physiological and molecular changes, including alterations in the plant metabolic profile. These changes may play a beneficial role in protecting cells during cold stress or before freezing temperatures occur (Thomashow, 1999).

Lipid composition changes and lipid metabolism during cold stress are crucial in determining the extent of cold damage in plants and other species. Increased levels of unsaturated fatty acids in the plasma membrane of acclimated plants enhance membrane fluidity and stability. Studies using fatty acid desaturase (fad2) mutants have demonstrated that polyunsaturated lipids are necessary for survival at cold temperatures in *Arabidopsis* (Miquel et al., 1993). In cold-acclimated rye (*Secale cereale* L.), the levels of di-unsaturated molecular species such as phosphatidylcholine and phosphatidylethanolamine were found to increase in the plasma membrane (Lynch and Steponkus, 1987). Similar findings have been reported in tea (*Camellia sinensis*) (Li et al., 2020) and banana plants (*Musa* spp.) (Zhang et al., 2011). Interference in the sucrose mechanism under cold stress may cause developmental aberrations in plants, leading to a decrease in the activity of the cell wall invertase enzyme. This results in sucrose accumulation and, consequently, prevents cell division in the endosperm (Cheng et al., 1996).

In conclusion, cold stress has significant effects on various physio-biochemical processes in plants. Exposure to low temperatures can lead to decreased photosynthetic efficiency, transpiration, and stomatal conductance, as well as increased levels of ROS and MDA. These changes ultimately result in reduced root and shoot growth. However, plants have defense mechanisms such as osmotic regulation and antioxidant enzymes to counteract the detrimental effects of cold stress. Osmotic adjustments and the accumulation of osmo-protectants and antioxidants help protect cell structure and maintain turgor, enhancing plant tolerance to cold stress. Cold stress also influences gene expression patterns, protein synthesis, and lipid composition, affecting membrane fluidity and permeability. The activity of enzymes like SOD, APX, CAT, and GR increases in response to low temperatures, while the accumulation of MDA serves as an indicator of oxidative stress sensitivity and cold tolerance. Furthermore, interference in the sucrose mechanism under cold stress can lead to developmental aberrations in plants. Overall, understanding the physiological and molecular changes induced by cold stress is crucial for developing strategies to enhance plant cold tolerance and mitigate the negative impacts of low temperatures.

The role of phytohormones in gene regulation to cold tolerance

Phytohormones, such as abscisic acid (ABA), auxins (IAA), gibberellins (GAs), cytokinins (CKs), salicylic acid (SA), ethylene (ET), brassinosteroids (BRs), and jasmonic acid (JA), play a crucial role in mediating cold stress signaling and regulating the transcription of certain cold-regulated (COR) genes (Deng et al., 2018). When plants experience cold stress, the levels of ABA and JA in the leaves increase, while ET, CKs, and GA decrease. After exposure to cold stress, the concentration of JA increased by up-regulating the expression of JA biosynthetic genes, which positively impacted cold stress tolerance in *Artemisia annua* (Liu et al., 2017). The exogenous application of JA significantly improved plant freezing tolerance in *Arabidopsis*, while blocking endogenous JA biosynthesis and signaling decreased plant freezing stress tolerance. Correspondingly, the production of endogenous JA increased after exposure to cold stress (Hu et al., 2013). In addition, several JAZ proteins, repressors of the JA signaling pathway, physically interact with ICE1 and ICE2 and repress their transcriptional functions. Overexpression of JAZ1 and JAZ4 repressed freezing stress responses in *Arabidopsis* (Hu et al., 2013). GAs have various functions in regulating plant growth processes (Colebrook et al., 2014). Besides growth regulation, GAs can also coordinate plant growth and stress responses to contribute to cold resistance by reducing GA levels and signaling after exposure to cold stress (Colebrook et al., 2014). Overexpression of OsSLR1, which encodes a rice DELLA protein, enhanced chilling tolerance by mediating SLR1 physically interacting with OsGRF6 to increase OsGA2ox1 expression and decrease GA content (Li et al., 2021). Low temperature-induced CBF1 expression results in an increase in DELLA protein accumulation by decreasing GA content. CBF1 enhances freezing tolerance through the synergistic DELLA-dependent and COR-dependent pathways (Achard et al., 2008). Additionally, DELLA proteins act as repressors of the GA hormone signalling pathway, and **GRF** modulation contributes to cold stress-responsive gene expression (Lantzouni et al., 2020). Phytohormones also have a significant impact on starch and glucose metabolism and the inhibition of ROS (An et al., 2012). The role of SA in plants can vary depending on the level and severity of abiotic stress.

At moderate and severe levels of abiotic stress, SA has been attributed to redox regulation in plant cells (Yuan and Lin, 2008) and the protection of cell structures under cold stress (Zhang et al., 2007). SA plays crucial roles in response to external stimuli and activates the defense system in plants. The activation of phospholipase D is an early response to low temperatures and is involved in the accumulation of free SA, as well as the development of thermotolerance induced by low-temperature acclimation in grape berries (*Vitis vinifera*) (Wan et al., 2009). SA in plants promotes growth, ripening, and tolerance to abiotic stresses (Perez-Llorca et al., 2019). Various studies have demonstrated that foliar application of salicylic acid on different plants enhances cold stress tolerance. For instance, in *Solanum lycopersicum*, applying 0.2 mM salicylic acid during the fruit formation stage increased the levels of antioxidant enzymes, malondialdehyde, and proline contents, thereby enhancing cold tolerance (Ding et al., 2015). The response factors of ethylene primarily participate in the plant's response to biotic and abiotic stress. Han et al. (2020) isolated an ERF gene (MbERF11) from Siberian crabapple (*Malus baccata* Borkh.). When transformed into transgenic *Arabidopsis*, MbERF11 enhanced cold and salt tolerance by increasing the activities of antioxidant enzymes such as CAT, POD, and SOD, as well as the levels of photosynthesis pigments such as chlorophylls and proline contents. Additionally, it decreased the MDA content and scavenged ROS (Han et al., 2021). ABA plays a pivotal role as a hormone in regulating cold stress responses in plants. In *Cynodon dactylon*, the application of exogenous ABA has been shown to enhance cold tolerance by preserving cell membrane stability and modulating the expression of ABA and cold-related genes such as ABF1, CBF1, and LEA (Huang et al., 2017). Moreover, the ectopic overexpression of the ABA receptor OSPYL3 in *Arabidopsis* has been demonstrated to improve cold tolerance (Lenka et al., 2018). Low temperatures reduce water availability in plant cells, leading to osmotic stress and the stimulation of ABA biosynthesis (Chen et al., 2021). Endogenous abscisic acid is then transferred from the roots to the shoots, where it accumulates in the guard cells, causing water to escape and resulting in stomatal closure. Consequently, transcription and cell growth are reduced (Llanes et al., 2015). In *Triticum aestivum*, the application of exogenous ABA has been found to enhance cold tolerance by increasing the activities of various antioxidant enzymes. These enzymes include CAT, SOD, POD, APX, GR, dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase (MDHAR) (Yu et al., 2020).

In conclusion, phytohormones play a crucial role in mediating cold stress signaling and regulating

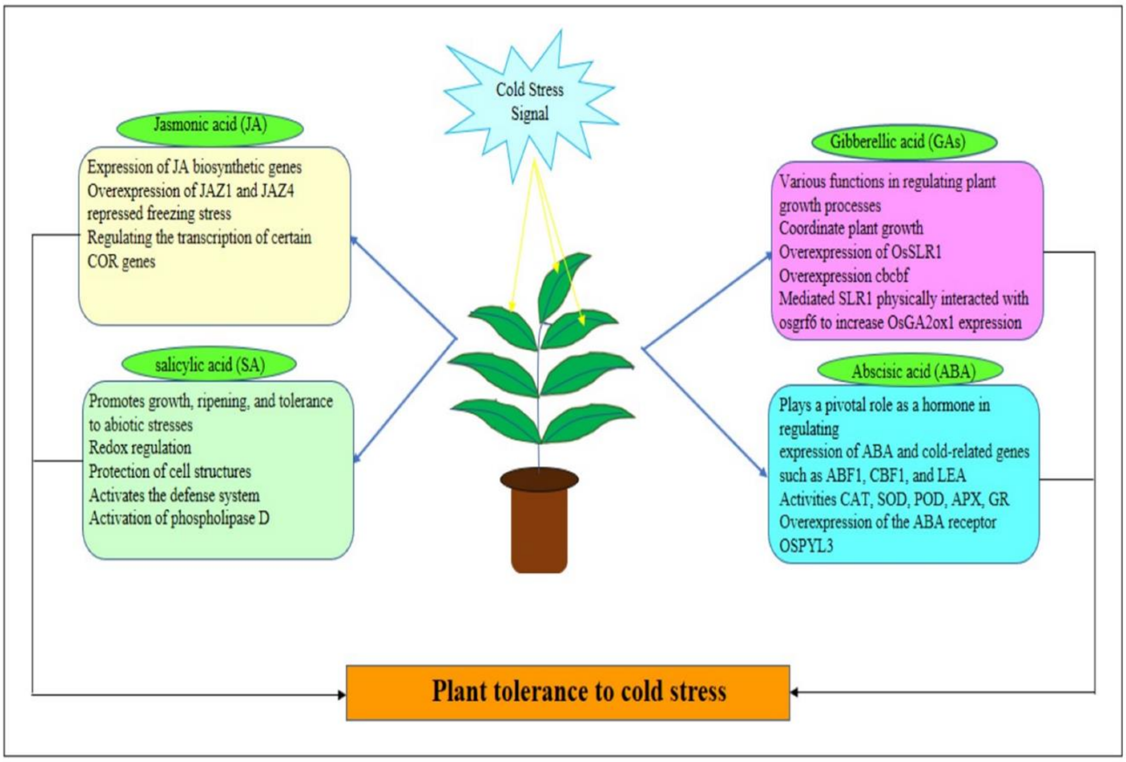

Fig. I. An overview of some phytohormones involved in regulating stress responses and altering external and internal responses under cold stress

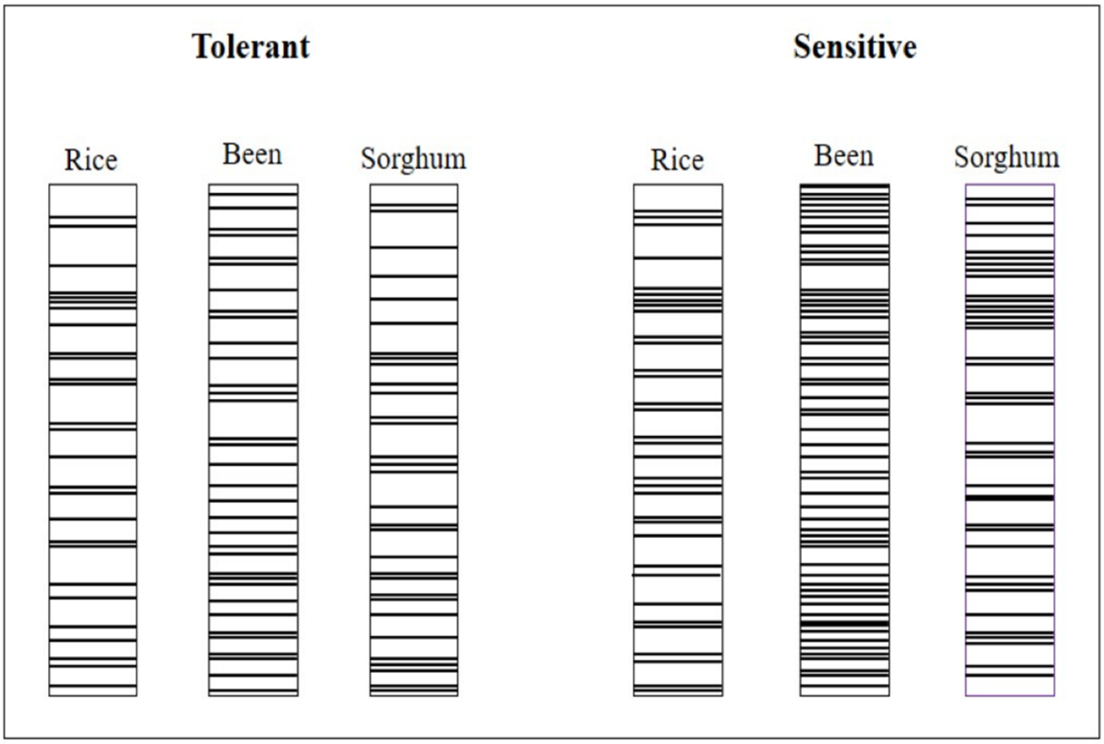

Fig. II. Genome mapping of cold stress-modulated genes of key categories involved in abiotic stress responses in common in tolerant and sensitive genotypes

gene expression in plants. Various phytohormones, such as ABA, IAA, GAs, CKs, SA, ET, BRs, and JA, significantly influence plant responses to cold stress. Under cold stress conditions, ABA and JA levels increase, while ET, CKs, and GA levels decrease. The increased levels of JA enhance cold stress tolerance, while JAZ proteins act as repressors of freezing stress responses. GAs not only regulate plant growth but also contribute to cold resistance by reducing GA levels and signalling. SA is involved in redox regulation and the protection of cell structures under cold stress, while ethylene plays a role in the plant's response to both biotic and abiotic stresses. ABA, in particular, regulates cold stress responses by maintaining cell membrane stability and modulating gene expression. Additionally, exogenous applications of ABA have been shown to enhance cold tolerance by increasing the activities of antioxidant enzymes, particularly in wheat (Fig. I).

Cold tolerant genes

Cold stress activates multiple downstream signaling pathways in plant cells, most notably the ICE1-CBF-COR (inducer of CBF expression-C-repeat-binding factors-cold-regulated genes) transcription cascade (Shi et al., 2015; Ding et al., 2015; Yang, 2022). This cascade induces the formation of complexes, such as CBFs/DREBs, that bind to the promoters of COR genes, initiating their transcription (Fig. 2). These signaling pathways lead to the activation of multigene families associated with transcription factors (TFs) like MYB, WRKY, NAC, bZIP, and APETALA2/ethylene-responsive element binding factor (AP2/ERF), which are crucial for stress responses (Wang et al., 2020; KidokoroH et al., 2021; Song et al., 2021).

During cold acclimation, low molecular mass polypeptides (15 to 32 kDa) accumulate in the leaf apoplast of plants such as winter rye and spruce (Marentes et al., 1993; Jarzabek et al., 2009). These polypeptides likely enhance cold tolerance by lowering the freezing point in the apoplastic space during cold stress. Being sessile, plants exhibit a broad range of gene expression patterns to tolerate cold stress and adapt to changing environmental conditions. The severity of cold stress decreases over time as plants undergo physiological, biochemical, and molecular changes (Dalmannsdottir et al., 2017).

In two of four analyzed datasets (rice 1 and rice 2; *Oryza sativa L.*), genes related to cell walls were upregulated in both cold-sensitive and one cold-tolerant genotype (*Sorghum bicolor L.*). Genes linked to secondary metabolism were upregulated in cold-sensitive *Vigna unguiculata* subsp. *Sesquipedalis* and cold-tolerant sorghum. Conversely, genes related to protein synthesis were downregulated in tolerant rice 1, rice 2, beans, and sorghum, and also in sensitive rice 1, rice 2, and sorghum. No other common gene categories were modulated by cold stress across the datasets (Fig. II).

The ICE1-CBF-COR transcription cascade is a key signaling pathway triggered by cold stress. This cascade initiates the expression of CBF genes, which encode transcription factors that activate COR gene transcription. These responses are regulated by several TF families, including MYB, WRKY, NAC, bZIP, and AP2/ERF. Additionally, cold acclimation leads to the accumulation of low molecular weight polypeptides in the leaf apoplast, which may lower the freezing point, contributing to enhanced cold tolerance. Ultimately, plants exhibit a wide range of gene expression adjustments in response to cold stress, gradually reducing its severity through physiological, biochemical, and molecular changes. Differential gene expression patterns related to cell wall composition, secondary metabolism, and protein synthesis vary depending on the plant species and genotype in response to cold stress.

Plant growth and productivity

Cold stress significantly disrupts key processes related to plant growth and development, including seed germination, seedling vigor, and establishment (Hussain et al., 2018). It also causes deficiencies in water and nutrient uptake (Aroca et al., 2003) and reduces photosynthetic capacity, which is linked to disturbances in the source-sink exchanges of assimilates and an overaccumulation of reactive oxygen species (ROS) in various crop species (Hassan et al., 2021; Zhou et al., 2022). Low temperatures lead to modifications in the composition and structure of the photosynthetic membrane, resulting in increased brittleness and

Table 1
The effect of cold stress on some physiological, biochemical and yield of different crops

Trait	Species	Change (+, -)	°C	Effect of change on the plant (+, -)	Reference
Soluble sugar	rapeseed	+	-2	+	(Lei et al., 2019)
Lipid peroxidation	Wheat / Maize	+	6.9 – 3.4	-	(Lidon et al., 2001)
Super oxide dismutase	Wheat	+	4	-	(Bibi et al., 2020)
photosynthetic rate	tobacco	-	8	-	(Li et al., 2023)
Transpiration rate	tobacco	-	8	-	(Li et al., 2023)
Abscisic acid	rapeseed	+	0	-	(Lei et al., 2019)
Water use efficiency	*Stevia rebaudiana*	-	5	-	(Hajihashemi et al., 2018)
Total chlorophyll	Hot pepper	-	10	-	(Nandagopal and Shanmugam, (2022)
Grain yield	Wheat	-	0.1	-	(Liu et al., 2019)
Catalase and peroxidase	barley	+	7	+	(Mutlu2013)
Proline	Maize	+	5	+	(Wu et al., 2022)
Gibberellic acid	rapeseed	+	0	+	(Lei et al., 2019)

slower enzymatic reactions. This directly affects the photosynthetic apparatus, lowering photosynthetic efficiency and causing the production of excess ROS (Liu et al., 2018). Studies have shown that cold stress can either up-regulate or down-regulate proteins involved in photosynthesis, such as chlorophyll a/d-binding protein and photosystem II reaction center proteins (Liang et al., 2007; Yamasaki et al., 2002). Furthermore, cold stress severely damages crop yield formation, starting with reproductive phase impairments characterized by sterile pollen, aborted ovules, and undersized grains, ultimately reducing final yields (Arshad et al., 2017; Zhang et al., 2019). This cold sensitivity can cause yield losses of 30-40% in rice and up to 78% in wheat, primarily due to reproductive disturbances and later grain development issues at temperatures below 10°C (Subedi et al., 1998). During the reproductive stage, low temperatures may result in flower drop, pollen sterility, and reduced fruit formation, which further decreases plant yield (Albertos et al., 2019).

Cold stress can lead to irregular distribution of pods and grains along the stem, with reduced pod formation occurring when night temperatures drop below 8°C (Gass et al., 1996). The response to cold stress and pod formation varies among different soybean cultivars, with gene expression regulation playing a crucial role in cold tolerance (Takahashi and Shimosaka, 1997). Additionally, low temperatures can induce early flowering through vernalization, a process that affects active and dividing cells beyond the meristem regions (Wellensiek, 1964). Vernalization is a phenological response to cold, delaying the transition from the relatively cold-tolerant vegetative stage to the more sensitive reproductive stage until milder temperatures are encountered (Kosova et al., 2008).

In wheat, cold temperatures affect phenology and grain filling, prolonging the vegetative phase before flowering (Subedi et al., 1998). The deposition of reserve nutrients during grain filling is also influenced by fluctuating environmental conditions, which can significantly impact both the quantity and quality of yield (Yang and Zhang, 2006).

In conclusion, cold stress has a direct impact on the photosynthetic apparatus, reducing photosynthetic efficiency and increasing the production of reactive oxygen species (ROS). Proteins involved in photosynthesis may be either up-regulated or down-regulated in response to cold stress. Additionally, cold stress negatively affects crop yield formation, starting with reproductive impairments and ultimately leading to reduced final yields. Rice and wheat, in particular, are highly sensitive to cold stress, with substantial yield losses reported.

Cold stress also causes irregular pod and grain distribution along the stem, and the effects on phenology and grain filling further exacerbate the decline in yield. Lastly, vernalization triggered by cold temperatures delays the transition from vegetative to reproductive stages, allowing plants to avoid entering sensitive phases until temperatures are more favorable.

Conclusion and Future Prospects

In recent years, significant advancements have been made in understanding how plants respond to cold stress, encompassing physiological, biochemical, and molecular aspects. Cold stress is a major climatic challenge that negatively impacts crop productivity and food security. However, the precise mechanisms by which plants sense and respond to cold signals remain elusive.

When exposed to low temperatures, plants activate cold responses through both CBF-dependent and CBF-independent pathways. The CBF1 transcription factor enhances freezing tolerance through synergistic DELLA-dependent and COR-dependent pathways. While considerable progress has been made in understanding these cold signaling pathways, the molecular mechanisms underlying cold signal perception and transduction still require further investigation.

Cold stress can decrease the photosynthetic rate, transpiration rate, total chlorophyll content, and water use efficiency. These changes can lead to reduced grain yield and productivity. Additionally, cold stress increases the levels of soluble sugars, proline, lipid peroxidation, and enzyme activities such as catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD), as well as the content of gibberellic acid (GA) and abscisic acid (ABA) in crops (Table 1).

Plant hormones, including salicylic acid (SA), jasmonic acid (JA), ABA, and gibberellic acid (GA), play a crucial role in enhancing cold resistance. They do so by increasing soluble sugars, soluble proteins, and proline, scavenging reactive oxygen species (ROS), and activating the antioxidant defense system.

One proposed mechanism for cold signal perception involves the plasma membrane. It is hypothesized that changes in membrane fluidity and ion channel activity may be involved in sensing and transmitting cold signals within the plant. However, further research is necessary to fully elucidate these processes.

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