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Chapter

Effect of Low-Temperature Stress on Plant Performance and Adaptation to Temperature Change

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Abstract

Low-temperatures (LT) stress is one of the abiotic stresses in plants that affect cell survival, cell division, photosynthesis, and water transport, negatively affecting plant growth, and eventually constraining crop productivity. LT stress is categorized as, (i) chilling stress where low temperature (0–15°C) causes injury without ice crystal formation in plant tissues, and (ii) freezing stress (<0°C), where ice formation occurs within plant tissues. Both stresses are together termed low temperature or cold stress. In general, plants originating from tropical and subtropical regions are sensitive to LT, whereas temperate plants showed chilling tolerance to variable degrees. Low-temperature stress negatively impacts plants, may affect the survival rate of crop plants, and also affect various processes, including cell division, photosynthesis, plant growth, development, metabolism, and finally reduce the yield of crop plants, especially in the tropics and subtropics. To overcome stress generated by low-temperature exposure, plants trigger a cascade of events that enhance their tolerance by gene expression changes and activation of the ROS scavenging system, thus inducing biochemical and physiological modifications. In this chapter, a detailed discussion of different changes in plants and their tolerance mechanism is done to understand the plant's response under LT stress.

Keywords: low-temperature stress, oxidative stress, resilience, stress tolerance

1. Introduction

Low-temperature (LT) stress is one of the abiotic stresses [1] in plants that affect cell survival, cell division, photosynthesis, and water transport with a negative effect on plant growth, eventually constraining crop productivity [2, 3]. LT stress is categorized as, (i) chilling stress, where low temperature (0–15°C) causes injury without ice crystal formation in plant tissues, and (ii) freezing stress (<0°C), where ice formation occurs within plant tissues. Both stresses are termed low temperature or cold stress [4]. In general, plants originating from tropical and subtropical regions are sensitive to LT, whereas temperate plants showed chilling tolerance to variable degrees [2]. Low temperature negatively impacts plants, may affect the survival rate of crop

plants, and also affect various processes including cell division, photosynthesis, plant growth, development, metabolism, and finally reduce the yield of crop plants, especially in the tropics and subtropics [5, 6]. To overcome stress generated by LT exposure, plants trigger a cascade of events that enhance their tolerance by changes in gene expression and activation of the ROS scavenging system and thus inducing biochemical and physiological modifications [7, 8]. This review is a detailed discussion of different changes in plants and their tolerance mechanism in order to understand the plant's response under LT stress.

2. Morpho-physiological changes in crop plants in response to LT stress

Morphological changes are the change that is visible on the plants during the early stage of LT stress. These are the primary signs of the plants, indicating adverse effects of stress on plants. Stress reduces leaf expansion, causes chlorosis, wilting of leaves and necrosis, and accelerates senescence in crop plants [9, 10]. Various metabolic reactions were inhibited by LT exposure, consequently preventing the plant's full genetic expression potential expressed by diverse phenotypic symptoms [11]. Low temperature is a limiting factor for seed germination and plant growth [12–14]. Under LT stress in *Elymus nutans* Griseb, the shoot and root lengths in tolerant seedlings were longer than the susceptible ones. Low temperatures also increased the mortality percentage of seedlings [15]. LT dramatically affects photosynthesis as well [16]. The negative impact of abiotic stress on the photosynthetic process in plants has been extensively studied and measurement of chlorophyll fluorescence (Fv/Fm) has proven as an effective, reproducible, and nondestructive tool for evaluating the susceptibility index of plants subjected to LT stress [3, 17]. Under LT stress, photosynthesis is impaired, resulting in a lower amount of carbohydrates for grain production and reducing growth, adding to indirect yield loss [3]. In rice seedlings, LT stress affected total chlorophyll (Chl) content and thus photosynthetic efficiency [18, 19]. Proteomic analysis in a semihardy winter wheat cultivar under natural field conditions indicated a down-regulation of several photosynthesis-related proteins (such as oxygen-evolving enhancer protein, NADH dehydrogenase, and dehydroascorbate reductase) during the initiation of cold acclimation [16]. Low temperature decreases photosynthesis due to partial stomatal closure, slowdown of electron transport, inhibits metabolism of carbohydrates, and interferes with phloem loading [13]. In plants, the content of both total Chl and chlorophyll b (Chl b) decreased and the Chl a/b ratio increased under low night temperature stress [17]. Low night temperature probably enhanced the activity of chlorophyllase enzyme in leaves and hence resulted in reduced Chl synthesis. Most of the Chl a, all the Chl b, and other pigments absorb light. They transfer that light energy to the reaction center but only a part of Chl a molecule can utilize that energy to perform the charge separation process. Plants maintain a relatively higher level of Chl a content, so that they can perform the process of photosynthesis normally and adapt themselves to cold stress. The cessation of growth ensuing from cold stress decreases the capacity of utilizing the energy and hence results in feedback inhibition of photosynthesis. In cold-acclimated winter annuals, Calvin cycle enzymes accumulate in higher amounts and effectively maintain the photosynthetic activity of plants. The Chl content and photosynthetic parameters like Fv/Fm had a positive correlation with chilling injury indices and have been utilized as a marker of cold tolerance in sugarcane [20]. Under dark chilling treatment, Fv/Fm significantly decreased in plants and after the recovery period, the Fv/Fm ratio

recovered to nearly that of the control levels [21, 22]. A greater decrease in Chl content in the cold-sensitive rice genotype was reported as compared to the cold-tolerant genotype under cold stress [23]. LT tolerant lines of rice, after stress, seedling height in both the lines remained unchanged over time; however, more tolerant seedlings (M202) exhibited a small increase in the root-to-shoot ratio [23].

Carotenoids are not considered photosynthetic pigments, but play important role in protecting the photosystems from damage. They have structural roles and act as natural antioxidants, quenching triplet Chl and singlet oxygen species, which are potentially harmful to the chloroplast [24, 25]. Carotenoids also maintain and stabilize thylakoid membranes from the damage caused by lipid peroxidation and cold stress [26]. In *Elymus nutans* seedlings, carotenoid content was decreased when exposed to cold stress at 5°C. The decrease in carotenoid content was higher in GN (more sensitive) than DX (tolerant) seedlings [15].

In conclusion, under LT stress plants showed various phenotypic symptoms, these are the primary symptoms of stress. Photosynthetic pigments and photosynthetic parameters like Fv/Fm ratio are altered under LT stress and showed a positive correlation with the chilling injury indices and potential to be used as a marker for cold resistance.

3. Oxidative stress

Plants exposed to LT stress undergo various metabolic and physiological changes and chilling stress ultimately leads to oxidative stress in plants, a physiological condition, where an imbalance occurs between the generation of reactive oxygen species [27] and their metabolism *via* enzymatic and nonenzymatic antioxidants [28]. Different types of reactive oxygen species (ROS) are accumulated under LT stress, which includes (a) singlet oxygen (1O_2), (b) superoxide radical ($O_2^{\cdot-}$), (c) hydrogen peroxide (H_2O_2), and (d) hydroxyl radical (OH^{\cdot}) [29]. In plant cells, ROS are continuously produced as a

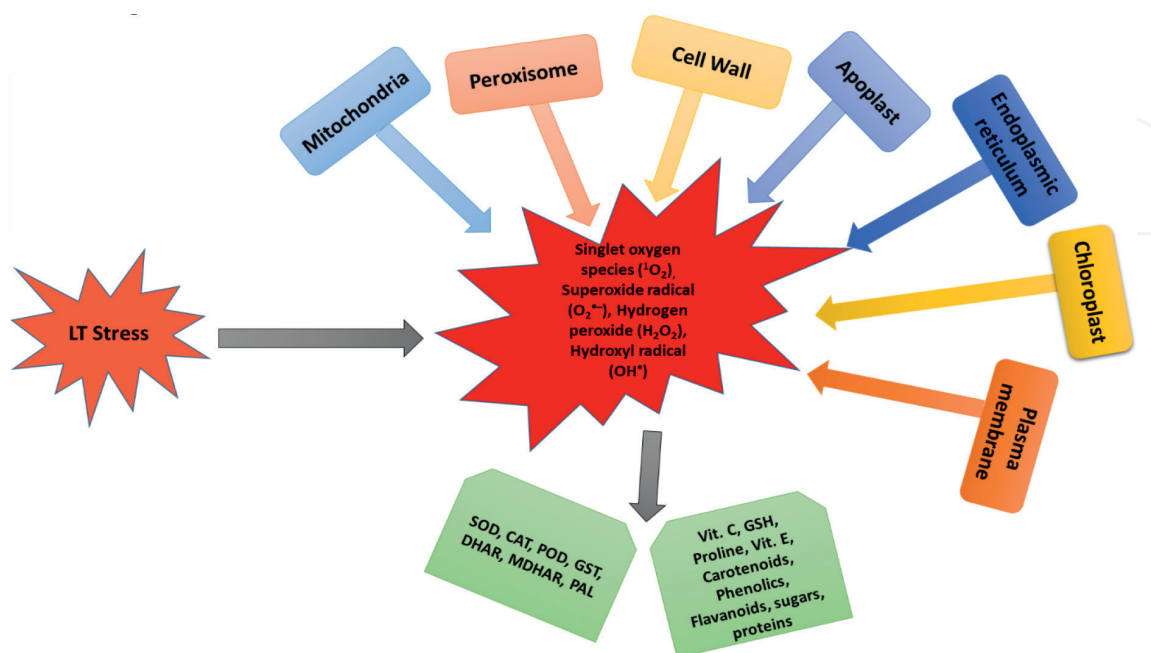


Figure 1.
Overview of oxidative stress, production of reactive oxygen species, and its scavenging.

consequence of aerobic metabolism in all the intracellular organelles, particularly in the chloroplast, mitochondria, and peroxisomes [30]. Chloroplast is considered the main source of ROS in plants. Other ROS-producing sources include NADPH oxidases, cell wall-bound peroxidases, and amine oxidases (**Figure 1**).

4. Other biochemical changes

Under normal physiological conditions, ROS levels are maintained low by the action of various enzymatic and nonenzymatic antioxidants, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione (GSH), and vitamin C [31]. Accumulation of ROS accelerated under extremely cold conditions, beyond the plant's tolerant level due to less activity of antioxidant enzymes, which are responsible for detoxification of ROS. Higher content of ROS causes oxidative stress which is manifested as peroxidation of membrane lipids, damage to proteins, carbohydrates, and DNA, etc. [28, 32, 33]. They also alter enzyme activities, biochemical reactions, and plant processes, such as photosynthesis and respiration, which negatively affect the plant's survival percentage [12].

ROS alters the activities of enzymes and affects various biochemical reactions and physiological processes, including nutrient movements, respiration, photosynthesis, and transpiration, thus having a negative impact on a plant's survival percentage. Higher H₂O₂ accumulation in cold-stressed leaves of chickpea plants resulted in membrane injury [34]. Oktem *et al.* [35] also stated that an increase in oxidative damage caused by cold stress in lentils resulted due to high H₂O₂ production. Higher MDA content and higher electrolyte leakage from cell membranes of sensitive plants indicate injury caused by LT stress [36, 37]. Increased content of ROS and malondialdehyde (MDA) under LT stress probably impair metabolism in rice seedlings [38]. A significant increase in lipid peroxidation, membrane leakage, and hydrogen peroxide levels was observed in wheat seedlings subjected to chilling stress [39]. Apostolova *et al.* [40] reported a 40 and 100% increase in the content of H₂O₂ in the leaves of winter wheat and spring wheat, respectively under cold stress. Janmohammadi *et al.* [41] reported that during cold stress less cold-hardy spring wheat cultivar had a higher accumulation of hydrogen peroxide than the winter wheat cultivar. LT stress resulted in increased electrolyte leakage in the leaves of *Avena nuda* L. (naked oats) seedlings. Electrolyte leakage also increased with the prolongation of the stress period [42]. Membranes are a primary site of cold-induced injury because of their central role in the regulation of various cellular processes [43, 44]. LT stress leads to the destruction of cell membrane structure in maize plants [45], change the permeability of membranes, and causes leakage of cell electrolytes [5] and thus damages the plants. It has been demonstrated that LT responses are triggered by membrane rigidification, coupled with calcium influxes, cytoskeletal rearrangements, and the activation of MAPK cascades [46]. ROS are not only the toxic by-products of metabolism but also act as signaling molecules that transform the expression of different genes, for example, genes encoding for antioxidant enzymes and modulators of H₂O₂ production. ROS plays a vital role in plant stress acclimation [47, 48].

In conclusion, ROS are accumulated under LT, which alter the activities of enzymes, affect various biochemical, and physiological processes, and thus affect the plant's survival. Enzymatic and nonenzymatic antioxidants enhance their content under LT stress and are involved in the detoxification of ROS, thus increasing the resistance against the stress condition.

5. Enzymatic antioxidants

Plants have developed ROS scavenging mechanisms, which include a variety of nonenzymatic and enzymatic defense systems to protect cellular membranes and organelles from the damaging effects of ROS [49, 50]. Types of antioxidants produced in the plants are represented in **Table 1**. The degree of damage by ROS depends on the balance between the accumulation of ROS products and their detoxification by the antioxidant scavenging system [49].

The efficiency of the antioxidant defense system to scavenge ROS largely decides the plant's sensitivity to chilling [27, 28, 54]. A higher amount of H₂O₂ produced during stress is detoxified by APX, POD, and CAT in different organelles [48]. Catalase converts H₂O₂ into O₂ and water. Zhao *et al.* [54] reported in tomato cultivars that higher activities of CAT, APX, POX, and SOD could be positively correlated with chilling tolerance. The CAT activity increased in plants under prolonged LT stress [55]. Fahimirad *et al.* [56] recorded an increased CAT activity in canola cultivars in response to LT stress. The increase in activity was higher in winter canola than LT-sensitive spring canola. The LT stress resulted in enhanced peroxidase activity in naked oats (*Avena nuda* L.) [42]. Dai *et al.* [57] observed that after 72 hours of the recovery period, in barley seedlings, the peroxidase activity was significantly higher in the cold-tolerant cultivar (M₀103) in comparison to the cold-sensitive cultivar (Chumai). Aydin *et al.* [58] reported that in tomato plants (*Lycopersicon esculentum* L.) highest MDA production occurred after 10 days of stress and SOD enzyme activity gradually increased with increasing exposure to cold stress. Expression of the SOD gene and enzyme plays a key role to provide resistance in tomato plants against cold stress. Zhang *et al.* [59] observed that in *C. Sativus*, activities of antioxidant enzymes *viz.* SOD, POD, CAT, and APX were reduced after chilling exposure. Fahimirad *et al.* [56] reported that cold stress exposure enhanced SOD activity by 2.5-fold in winter canola (tolerant) leaves when compared to controls, whereas spring canola (LT sensitive) cultivar showed a 1.7-fold increase. Sun *et al.* [60] reported that in sugar cane seedling roots at 4°C, SOD activity was higher in cold tolerant (GT28) variety than cold-sensitive (ROC22) variety. Various studies showed a similar response to cold stress in wheat [61], strawberries [62], and barley [63]. Hajiboland and Habibi [64] reported that in cold-treated seedlings, the activity of SOD increased significantly, while in the acclimated seedlings, SOD activity did not differ from the control.

CAT and POD are important enzymes that scavenge H₂O₂ [65]. Generally, there is a positive correlation between stress tolerance and the activity of POD, CAT, and SOD enzymes in plants [65]. Javadian *et al.* [61] reported that cold-tolerant wheat cultivars had higher CAT activity. Fahimirad *et al.* [56] reported that winter canola had a greater increase in CAT activity than LT-sensitive spring canola under LT stress.

Antioxidant	Types
Enzymatic antioxidants	Catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione peroxidase (GPX), glutathione reductase (GR), glutathione S-transferase (GST), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), etc. [13, 51–53].
Nonenzymatic antioxidant	Ascorbic acid (Vitamin C), α-tocopherol (Vitamin E), glutathione (GSH), carotenoids, phenolics, and flavonoids, etc. [13, 51–53].

Table 1.

List of the different types of enzymatic and nonenzymatic antioxidants of plant.

Morsy *et al.* [66] reported that under cold stress no change was recorded in peroxidase activity in cold-tolerant as well as cold-sensitive rice seedlings. Liu *et al.* [42] reported that POD activities in naked oats (*Avena nuda* L.) were higher under LT than normal temperature. But with time POD activities decreased greatly, indicating that LT had affected POD enzyme synthesis. Dai *et al.* [57] reported that in two contrasting cold-tolerant cultivars of barley, the tolerant cultivar (M0103) had significantly higher peroxidase activity than the sensitive cultivar (Chumai) after 72 h recovery in cold-treated plants. POD activity increased in *Cucumis sativus*, tomato, and canola under LT stress [61, 67, 68]. Sun *et al.* [60] reported that under LT stress at 4°C POD activity was increased in the roots of sugarcane seedlings than in control. The increase in POD activity was higher in the cold-tolerant genotype (GT28) than cold-sensitive genotype (ROC22). Higher POD and SOD activity probably suggest their possible role in mitigating adverse environmental damage. Hajiboland and Habibi [64] reported a slight increase in CAT activity in both wheat cultivars under chilling temperatures with and without acclimation. In contrast, POD activity increased in spring wheat cultivar but not in winter wheat by both temperature treatments. Gong *et al.* [69] reported that in maize seedlings, cold acclimation enhanced the activity of five antioxidant enzymes catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and glutathione reductase (GR). In conclusion, enzymatic antioxidants accumulate under LT stress and are actively involved in the detoxification of ROS thus enhancing the resistance of the plants.

6. Nonenzymatic antioxidants

In plants ascorbic acid (AsA) and glutathione (GSH) are low molecular weights, nonenzymatic antioxidants, abundantly present, and participate in ROS scavenging [28, 70]. The tripeptide glutathione (γ -glutamyl-cysteinyl-glycine) is widely distributed in plant cells and is implicated in the adaptation of plants to environmental stresses, such as extreme temperatures [48]. It is an important antioxidant associated with the regeneration of AsA in the ascorbate-glutathione cycle and participates in the removal of H₂O₂ [67]. Its antioxidant activity is mainly due to its redox buffer property. It functions to remove toxic peroxides formed in the cell during normal and stressed conditions [70, 71].



Glutathione detoxifies ROS in concert with NADPH. At low nonfreezing temperatures, several plants accumulate GSH and show an increase in GR activity, indicating a possible role in enhancing chilling tolerance and cold acclimation. A differential elevation in GSH has been reported in a number of LT-exposed plants, including cucumber genotypes [72, 73].

Ascorbic acid (AsA) is one of the universal nonenzymatic water-soluble antioxidants having a substantial potential of scavenging ROS in plants both under stressed and non-stressed conditions [74]. Cell cytoplasm constitutes the most abundant pool of ascorbate, while to some extent it is also transported across the plasma membrane (usually 5%) to the apoplast [75, 76]. Ascorbate is a component of the NADPH/glutathione/ascorbate cycle that removes photosynthetically generated O²⁻ and H₂O₂. It may also directly reduce O²⁻, quench ¹O₂ and regenerate reduced tocopherol. Lukatkin

and Anjum [77] reported that AsA and GSH have a high potential for sustainably increasing chilling resistance in plants. A significant increase in the levels of these antioxidants as well as the activity of NADPH-generating dehydrogenases have been caused by LT stress [78]. The AsA content was more in tolerant chickpea (*Cicer arietinum*) genotypes after chilling at the reproductive phase [79]. Kim *et al.* [80] reported that changes in GSH content in two rice cultivars were not evident until 10 days of cold stress. Ascorbic acid content increased significantly in stressed IR50 seedlings in comparison to the control while M-202 stressed seedlings showed little or no change. Overexpression of SIGMEs (*Solnaum lycopersicon*, GDP-Mannose 3', 5'-epimerase) was reported to cause AsA accumulation with enhanced cold tolerance in tomatoes [81]. Airaki *et al.* [78] reported that in pepper plants LT stress caused a significant increase in the level of soluble nonenzymatic antioxidants; ascorbate and glutathione. Kader *et al.* [39] reported an increase in GSH and free ascorbate content in 15 days old seedlings of two wheat varieties after cold treatment. Esra *et al.* [82] reported proline accumulation in two pepper variety seedling leaves under cold stress as compared to control counterparts. Yadegari *et al.* [83] reported that proline content increased more under acclimation than non-acclimated seedlings of soybean and hence provide more tolerance. Zuther *et al.* [84] reported that proline content was higher in acclimated leaves of *Arabidopsis thaliana* than in non-acclimated leaves and recovered back to normal levels after de-acclimation. Airaki *et al.* [78] reported that in pepper plants LT stress significantly increased the levels of soluble nonenzymatic antioxidants; ascorbate and glutathione. Kim *et al.* [80] reported that LT stress at 9°C resulted in increased proline and glutathione content in IR50 rice seedlings, compared to controls, and change in glutathione content was evident on the 10th day of LT stress. Kim *et al.* [23] also reported similar changes, under LT stress for proline, glutathione, and ascorbic acid in rice seedlings. Zhang *et al.* [85] reported that to resist the effect of cold stress, resistant sugarcane varieties showed a higher accumulation of proline content in leaves than sensitive varieties. Sun *et al.* [60] reported an accumulation of proline content in sugarcane seedlings under cold stress. Krol *et al.* [86] reported that cold stress caused a decrease in the radical scavenging activity in the leaves of both varieties of grapes and the more-tolerant variety was characterized by better scavenging activity. In conclusion, nonenzymatic antioxidant accumulates in plants under LT stress and are involved in the detoxification of ROS, thus enhancing the resistance of plant against stress.

Phenylalanine ammonia-lyase (PAL) is the key enzyme of the phenylpropanoid pathway, converting L-phenylalanine (substrate) into *trans*-cinnamic acid, a precursor of phenolics. The activity of the PAL enzyme increases in response to LT stress [87] and is considered to be one of the main lines of cell acclimation in plants against stress [88]. Phenolics protect plants against ROS by acting as antioxidants [89, 90]. Christopoulos and Tsantili [91] used a PAL inhibitor to prove the role of PAL in the accumulation of phenolics under cold stress. Chilling stimulates the expression of genes for phenylalanine ammonia-lyase (PAL) in cucumber seedlings [92]. Olenichenko *et al.* [93] studied the effect of cold stress on phenolic compounds in winter wheat (*Triticum aestivum* L.) leaves, which resulted in hardening and detected an increased level of phenolic compounds. In chilling stressed petunia leaves, it was observed that stress led to elevated antioxidant capacity and total phenolic content [94]. Hajiboland and Habibi [64] reported that PAL activity was increased in winter wheat cultivars under acclimation and more phenolic content accumulated in seedling leaves. The transcription level of PAL and phenolic content was higher in acclimated chickpea seedlings than in non-acclimated ones [37]. Chilling stimulates

the enzymatic activities and the expression of genes for phenylalanine ammonia-lyase (PAL) in cucumber seedlings [92]. Pennycooke *et al.* [94] reported that chilling stress leads to elevated total phenolic content and antioxidant capacity in petunia. Krol *et al.* [86] reported that cold stress caused a decrease in the phenolic content in the leaves of two varieties of grapes, though the more-tolerant variety was characterized by higher phenolic contents. Cold acclimation resulted in a higher accumulation of phenolics, which were positively correlated with the antioxidant capacity of plants. Flavonoids are a type of phenolics, that accumulated at higher rates in leaves and stems of LT-stressed plants, which are responsible for enhanced cold tolerance [95]. Ahmed *et al.* [96] reported that anthocyanin (a flavonoid) content increased in *Brassica rapa* under cold stress. Total phenols are also the components of the nonenzymatic antioxidant system and their content has been correlated with the stress tolerance capacity of plants [97]. Esra *et al.* [82] reported that in pepper (*Capsicum annum* L.) phenolics accumulated in seedling leaves under LT stress. In acclimated plants, enhanced PAL activity and accumulation of different phenolics are thought to play an important role in creating cold tolerance [37]. Schulz *et al.* [98] showed that flavonoid accumulation increased in *Arabidopsis thaliana* after cold acclimation and all acclimated plants performed better under cold stress.

Plants accumulate a variety of compatible solutes, including sugars, polyamines, glycine betaine, and proline, in response to cold and other osmotic stresses [13]. In LT-tolerant plants, such as barley, rye, winter wheat, grapevine, potato, chickpea, and *A. Thaliana*, a positive correlation between improved cold tolerance and accumulation of endogenous proline content was observed [99–101]. In order to enhance the stress tolerance level of plants, proline act as a mediator of osmotic adjustment, proteins, and membrane stabilizer, an osmotic stress-related genes inducer, and a ROS scavenger, so that plants can perform better under stress [99, 100, 102]. The most feasible roles of proline are to (a) maintain the acidity of cytosol, (b) maintain the NAD⁺/NADH ratio, (c) enhance photosynthetic efficiency of the photosystem II, and (d) inhibit peroxidation of membrane lipids [103, 104]. Proline accumulated in chilling stressed soybean seedlings [83]. Kim *et al.* [80] reported that in two rice cultivars (IR50 and M-202) proline content increased significantly in stressed IR50 seedlings in comparison to control seedlings, whereas in M-202, stressed seedlings showed little or no change. Cold-acclimated plants recovered faster than non-acclimated plants because of the higher accumulation of proline in acclimated plants.

Fernandez *et al.* [105] reported that carbohydrate metabolism has greater LT sensitivity than other photosynthetic components. Although the precise function of soluble sugars remains unclear, their accumulation in plants under a cold acclimation process suggests that sugars probably play an important role as signaling molecules, cryoprotectants, or osmoregulator [106]. Ruelland *et al.* [107] reported that sugars possess a positive correlation with cold stress tolerance. Sugars under LT stress contribute to preventing the water within the plant cells to freeze because of its typical compatible osmolyte property, hence reducing the availability of water for the ice nucleation process in the apoplast. Sugars replaced water molecules in establishing hydrogen bonds with lipid molecules and hence protecting plant cell membranes during cold-induced dehydration [107]. In addition to these, sugars may also play a role in scavenging reactive oxygen species and contribute to enhanced stabilization of membranes [108, 109]. Hormone signaling and sugar signaling are closely associated processes, which contribute to managing plant growth, development, and defensive responses against stress [110]. Seedling resistance against cold was enhanced when rice seedlings were pretreated with fructose or glucose [66]. Trehalose possesses a

unique capacity for reversible water absorption and appears to be superior to other sugars in protecting biological molecules from desiccation-induced damage [111]. Transgenic *A. thaliana* plants showed enhanced freezing tolerance due to the accumulation of trehalose during cold treatment [112].

Sucrose accumulated in higher amounts in LT-stressed plants [113]. Sucrose acts as an osmoprotectant, as it maintains the turgor pressure of cells and stabilizes cell membranes by interacting with phosphate in their lipid headgroups, decreasing membrane permeability [106]. In some plants, the increase in sucrose content can be as high as 10-fold. Lower amounts of other free sugars like glucose and fructose also get accumulated under stress. The LT exposure also leads to fructan synthesis in temperate grasses, which were reported to depend upon sucrose accumulation. The effects were studied on a less cold-hardy spring cultivar (pishtaz) and a cold-hardy winter cultivar (CDC-ospray) of wheat under cold acclimation (20 days at 4°C), interrupted by de-acclimation (10 days at 25°C) and then followed by re-acclimation conditions (10 days at 4°C). Hardening conditions induced the accumulation of carbohydrates in both cultivars and the de-acclimated plants exhibited a significant reduction [114]. Total soluble sugars, reducing sugars, and sucrose contents were higher in cold-acclimated than those in non-acclimated plants of sweet cherry [115].

Accumulation of carbohydrates under LT may be due to enhanced expression and post-translation activation of enzymes of the sucrose synthesis pathway [116] and fructose-1,6-bisphosphatase [115]. Sun *et al.* [60] also reported that in sugarcane seedling roots, soluble sugar content increased after LT stress and increased to a higher value in a cold-tolerant variety of sugarcane. Hajiboland and Habibi [64] reported that under cold stress and acclimation total soluble sugar content increased equally in winter wheat while sugar content was higher in acclimated spring wheat seedlings than in non-acclimated seedlings. Parteli *et al.* [117] reported in 1-year-old plants of coffee under a cold acclimation period, the soluble sugars accumulated and enhanced cold tolerance. Burchett *et al.* [118] reported that in cold-acclimated (at 5°C) winter barley plants, the sugar concentration was slightly lower than in non-acclimated plants. Sugars had a positive correlation with cold stress tolerance because they act as osmolytes and protect the water within the plant cells and reduce water accessibility for ice formation. Sugars also establish hydrogen bonds with lipids by replacing water molecules and hence protect the membranes during cold-induced dehydration. Sugars also act as ROS scavengers and play role in membrane stabilization [107]. Sucrose synthase (*Sus*) is one of the key enzymes involved in sucrose synthesis metabolism, especially in non-photosynthetic tissues. The reversible transformation of sucrose and UDP into UDP-glucose and fructose is catalyzed by the sucrose synthase enzyme. Under normal growth conditions, *Sus* activity has been linked to phloem loading-unloading and nodule function [115]. The differential regulation of stress-responsive *Sus* genes in leaves might represent part of a general cellular response to the allocation of carbohydrates during acclimation processes, such as the synthesis of cell walls and starch. Under normal physiological conditions, sucrose synthase has a very low level of expression and serves no apparent metabolic function. In leaves and various organs of plants, stress resulted in the stimulation of the expression of *Sus* gene(s) and enhanced stress tolerance. Turhan and Ergin [115] studied the effect of cold acclimation in sweet cherry. The activity of sucrose synthase was higher in the non-acclimated stage than those in the cold-acclimated stage. Klotz and Haagenson [119] studied the effect of cold stress on sugar beet roots and reported that sucrose synthase enzyme activity showed several-fold changes. Abdel-Latif [120] reported that cold shock in wheat seedlings caused an increase in sucrose synthase

enzyme activity. The accumulation of sucrose in cane sugar exposed to LT stress supports the role of this sugar as an osmoprotectant that stabilizes cellular membranes and maintains turgor pressure [121]. Yue *et al.* [122] reported that after cold acclimation total soluble sugars and specific sugars, including glucose, sucrose, and fructose, were constantly elevated during cold acclimation and decreased after de-acclimation in tea plants. Cowie *et al.* [123] reported that in *Arabidopsis thaliana* sucrose had a regulatory role in the acclimation of whole plants to cold and this may be important during diurnal dark periods. Zuther *et al.* [84] reported that sucrose content was higher in acclimated leaves of *Arabidopsis thaliana* than in non-acclimated leaves and recovered back to non-acclimated levels after de-acclimation. Burchett *et al.* [118] also observed that in winter barley plants acclimated at 5/−1°C; day/night, and there was a significant increase in the glucose, sucrose, and fructose content. The sucrose content increased by 4-fold in comparison to non-acclimated plants.

Low-temperature stress resulted in the synthesis of different types of proteins [13]. Proteins are the major players in most cellular events and are directly involved in plant LT responses [124]. Cold stress increased soluble protein content in pepper (*Capsicum annum* L.) varieties [82]. Different plant species have shown that cryoprotective proteins are encoded by a range of cold-induced genes. Specific proteins with antifreeze activity (antifreeze proteins, AFPs), accumulated during cold acclimation in the apoplast, thus enhancing plant resistance against freezing stress [125–127]. These AFPs were identified as chitinase-like proteins, β -1,3-glucanase-like proteins, thaumatin-like proteins, and polygalacturonase inhibitor proteins [127, 128]. They were also present in non-acclimated plants, but at different locations and did not exhibit antifreeze activity, which suggested that different isoforms of PR proteins are produced under LT. Until now, no plant has been reported to have constitutive antifreeze activity. However, different studies reported the accumulation of transcripts and translation products of AFP genes during cold acclimation [128]. A number of studies have shown that after exposure to LT, many PR genes get induced and enhanced disease resistance was observed in plants [129].

Xu *et al.* [130] found that frost-sensitive winter wheat cultivars exhibited high levels of ROS and leaf cell death in response to abrupt freezing stress, whereas significant increases in the relative abundance of antioxidant-related proteins were found in frost-tolerant cultivar leaves. Under LT stress in sugarcane seedling roots, the total soluble protein was higher in the cold-tolerant variety than cold-sensitive variety [60] and helped to tolerate LT stress. Moieni-Korbekandi [52] reported in canola (*Brassica napus* L.) seedling leaves that soluble protein content increased under cold stress. Esra *et al.* [82] reported that in two pepper (*Capsicum annum* L.) varieties total soluble protein content was higher under cold stress conditions. These proteomic results emphasize the assumption that freezing-tolerant plants are capable of managing ROS-mediated damage more efficiently than sensitive ones. Sarhadi *et al.* [131] investigated the interrelationship between vernalization fulfillment and expression of LT-induced proteins in wheat genotypes differing in freeze tolerance. Their results showed a clear induction of cold-regulated (Cor)/Lea and antifreeze proteins (AFPs) during cold acclimation in the freeze-tolerant genotype, whereas less induction was observed in the semi-hardy genotype. In winter rye seedlings one of the cold-induced thermal hysteresis proteins was β -1,3-glucanase [132]. Consequently, these proteins must possess extensive structural similarities with the pathogen-induced basic β -1,3-glucanase in tobacco. Cryoprotection increased linearly with an increase in β -1,3-glucanase concentration. Chang *et al.* [133] reported that the protein in the cell sap of cold-acclimated mungbean seedlings was 60% higher than control seedlings.

Yadegari *et al.* [83] reported that total protein content increased in both acclimated and non-acclimated seedlings of soybean.

Proteins with antifreeze activity were reported to be accumulated in the apoplast during cold acclimation, thereby offering plant resistance against freezing [127]. Winter rye antifreeze proteins (AFPs) enhance freezing tolerance by preventing physical damage caused by ice crystals and may also function as a barrier to inhibit ice formation [126]. These proteins were identified as β -1,3-glucanase-like proteins, and chitinase-like proteins [127, 128]. Their results interestingly revealed that during the cold acclimation process, the production of ice nucleation substances in both the leaf and the crown was suppressed, correlating with the rapid up-regulation of genes encoding the major anti-freeze (chitinases, glucanases, and thaumatin-like proteins) and ice recrystallization inhibition proteins. Antifreeze proteins (AFPs) or ice recrystallization inhibition (IRI) proteins ascribe to a category of proteins in plants that allow their survival in sub-zero situations. Sarhadi *et al.* [131] showed the expression of LT-induced proteins in wheat genotypes differing in freeze tolerance. Their results clearly showed the induction of cold-regulated (Cor)/Lea and antifreeze proteins (AFPs) during cold acclimation in the freezing-tolerant genotype. Comparable results were also observed in diploid wild wheat (*Triticum urartu* L.), where cold acclimation increased the abundance of ROS-scavenging proteins, LEA/RAB proteins, and dehydrins [134].

Species adapted by natural selection to LT environments have evolved a number of morphological, physiological, and biochemical means to improve survival under prolonged LT stress periods [135]. Cold-adapted species generally have short stature, small leaf surface area, and a high root /shoot ratio. Seedlings subjected to prolonged LT exposure showed chlorosis, wilting, reduced leaf expansion, necrosis, tissue

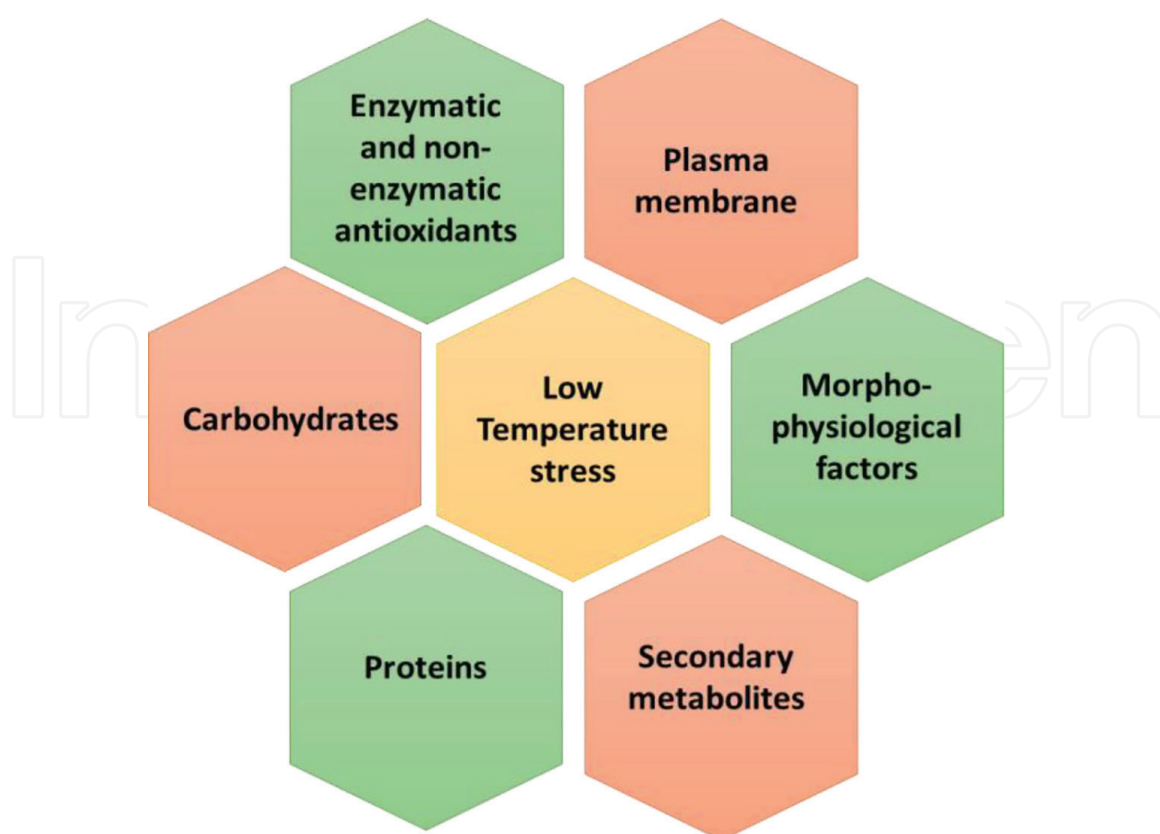


Figure 2.
Factors affected under low-temperature stress.

damage, and stunting [23]. Numerous studies indicated that an increase in antioxidants positively correlated with tolerance to LT stress in plants [23, 28, 136]. Fahimirad *et al.* [56] reported that winter canola had higher activity of antioxidant enzymes (SOD, CAT, and APX) and lower levels of MDA as compared to spring canola. The study showed a positive correlation between the activities of antioxidant enzymes and cold tolerance in the canola winter cultivar as compared to the spring cultivar. Sato *et al.* [137] reported that under cold stress, rice plants protected themselves from oxidative damage by increased production of various antioxidant species. Dai *et al.* [57] reported that LT-treated barley cultivars showed an increase in peroxidase activity after 72 hours of the recovery period. The activity of peroxidase in the tolerant cultivar (M₀103) was significantly higher than in the sensitive cultivar (Chumai). Liu *et al.* [42] reported that LT tolerance in *Avena nuda* L. was probably due to the higher content of proline, SOD, CAT, and POD activities. Cold stress conditions, caused a slight decrease in Fv/Fm ratio in plants that showed tolerance to cold, but a significant decrease was observed in plants that are sensitive to LT [138, 139]. Zhang *et al.* [140] reported that under 0°C treatment, plantlets of the tolerant genotype of strawberry showed a significant increase in peroxidase activity (**Figure 2**).

7. Cold acclimation

In several species, the acquisition of freezing tolerance can be induced by exposure to low, nonfreezing, and non-injurious temperatures [124, 141]. Acclimation may be defined as changes that occur in a plant in response to chilling temperatures, which confer subsequent tolerance to the cold injury [113], especially during germination and early seedling growth [69]. Cold priming/acclimation is associated with multiple physiological and biochemical alterations, including membrane stabilization, increased ROS and methylglyoxal (MG) detoxifications, activation of cold-sensitive protein kinases, NO and hormone biosynthesis, and accumulation of antioxidants, HSPs, cold-regulated proteins (CORs), and dehydrins [141–149]. Cold acclimation makes plants capable of protecting themselves from freezing-induced injury [149, 150]. Gong *et al.* [69] reported that in maize seedlings, cold acclimation resulted in higher survival percentage, catalase, ascorbate peroxidase, superoxide dismutase activity, and lower electrolyte leakage, than in non-acclimated seedlings. Cold acclimation in *Zoysia spp.* resulted in higher ABA and H₂O₂ levels as well as regulated antioxidant metabolism, resulting in improved freezing tolerance [151]. Cold priming-induced proline and glycine betaine accumulations were found to be associated with freezing tolerance in barley and *Arundo donax* L. [152]. Cold acclimation in *Arabidopsis thaliana* L. induced the accumulation of endogenous NO, and increased proline levels, conferring freezing tolerance [54]. Cold acclimation also enhanced the expression of genes that play role in membrane stabilization against freeze-induced damage [153, 154]. Minami *et al.* [155] verified that plasma membrane subfractions, responded to cold, by considerably changing lipid and protein composition in *Arabidopsis* plants. The study indicated that the plasma membrane is restructured in order to resist different stresses that take place throughout a freeze–thaw cycle. Cold acclimation increased the abundance of ROS-scavenging proteins, LEA/RAB proteins, and dehydrins in diploid wild wheat (*Triticum urartu* L.) [134, 156]. Studies have suggested that the activity of cold/chilling-induced genes may facilitate the metabolic changes that confer LT tolerance [156, 157]. Cold acclimation causes the synthesis of protective molecules, such as soluble sugars, sugar alcohols, proline,

and glycine betaine [106]. These molecules in conjunction with various proteins play a role to stabilize both phospholipids and proteins of the membranes and proteins of cytoplasm, maintain hydrophobic interactions between molecules and scavenge various types of ROS, which are produced under LT [158]. Some plants respond to LT by the synthesis of some specific proteins that are similar to plant pathogen-related (PR) proteins (particularly in winter rye), in response to cold and drought [159].

Kim *et al.* [23] reported that 14 days of LT stress killed most of the IR50 (sensitive) rice seedlings, while no negative effect was observed in M202 (tolerant) seedlings. Morsy *et al.* [66] showed that cold-tolerant seedlings of rice had 100% survival at 13/10°C regime in comparison to cold-sensitive seedlings, which suffered 50% mortality under the same conditions. Gong *et al.* [69] also reported that the percentage survival of maize seedlings increased after the pretreatment of seedlings at 1°C. Kargiotidou *et al.* [160] reported that the percentage survival of cotton is enhanced if plants are acclimated at low and nonfreezing temperatures prior to cold stress. Many studies in the literature have reported that LT stress affected seedling growth parameters viz. germination, and seedling growth, and caused chlorosis, wilting of leaves, reduced leaf expansion, and necrosis of tissue [12–14]. Low-temperature stress in *Elymus nutans* Griseb decreased shoot lengths of tolerant (DX) and sensitive (GN) genotypes by 88.8 and 91.7%, respectively compared to controls [15]. Jan *et al.* [161] showed that under cold stress one variety of rice SB showed no change in shoot length, while B-385 showed a slight decrease in average shoot length. Both the varieties showed some increase in root length under cold stress. Razmi *et al.* [162] reported that in sorghum (*Sorghum bicolor* L.) genotypes, LT reduced the germination percentage, root length, and shoot length of the seedlings, whereas increased the root/shoot ratio. Increased RL/SL under LT might be an indication of water deficit stress due to cold stress.

LT stress increased the chlorophyllase enzyme activity in grapevine leaves and restrained the synthesis of total Chl [163]. Plants need to maintain a sufficient level of Chl a content to perform the photosynthesis process to some extent even under stress [17]. Yadegari *et al.* [83] reported that under LT stress at 5°C in soybean seedlings Chl a, b, and total Chl contents decreased. However, Yang *et al.* [17] reported that in bitter melon genotypes, Chl a content increased, whereas total Chl and Chl b contents decreased under cold stress. Our results are supported by the work of Esra *et al.* [82] who reported that in two pepper varieties (*Capsicum annum* L.), Mert and KM-121, the content of Chl a and total Chl significantly decreased, while no significant change was found in the content of Chl b in response to LT stress. Tang *et al.* [20] also reported that under low LT stress in different sugarcane genotypes total Chl content decreased. Carotenoids are not considered photosynthetic pigments, but they play an important role in the protection of the photosystems and accumulate under LT. Carotenoids act as natural antioxidants by quenching triplet Chl and singlet oxygen species, which are potentially harmful to the chloroplast [24, 25]. Fu *et al.* [15] reported that under LT stress at 5°C in *Elymus nutans* seedlings, carotenoid content decreased. The decrease in carotenoid content was higher in GN (more sensitive) than DX (tolerant) seedlings. Gerganova *et al.* [164] reported that in tomato plants after cold treatment, a pronounced decrease was observed in carotenoids. Yadegari *et al.* [83] reported that Chl a, b, and total Chl decreased in both acclimated and non-acclimated soybean seedlings, but in cold-acclimated leaves, this decrease was lesser than in non-acclimated seedlings. It is well documented that photosynthetic apparatus is sensitive to several environmental stresses and PS II appears to be preferentially affected by chilling stress [165]. Fv/Fm reflects the susceptibility to damage of the photosystem II (PSII). Yang *et al.* [17] reported that in two bitter melon genotype

seedling leaves, the Fv/Fm ratio was hardly affected by cold stress, suggesting that LT did not affect the efficiency of PSII. Grapevine seedlings grown under LT stress showed different effects on photosynthetic efficiency [166]. Tang *et al.* [20], however, reported that LT stress in different sugarcane genotypes affected Fv/Fm ratio, which decreased with temperature and stress period. Decreased Fv/Fm ratio indicated that the photosystem was affected under LT stress in sugarcanes. Many researchers pointed out that there was a significant decrease in Fv/Fm ratio under dark chilling stress and after the recovery period the values recovered to control levels [21, 22]. Mishra *et al.* [167] reported that Fv/Fm decreased in both acclimated and non-acclimated samples of *Arabidopsis thaliana*, but the decrease was more in sensitive than tolerant types. Hajiboland and Habibi [64] reported that cold and acclimation both did not affect the Fv/Fm of winter wheat “Sabalan” while causing a significant reduction of Fv/Fm in “Zagros” spring wheat. Khaledian *et al.* [37] reported an accumulation of H₂O₂ under cold stress in the leaves of chickpea plants.

Yang *et al.* [17] also reported higher electrolyte leakage for the sensitive bitter gourd genotype (Y-106-5) than the less sensitive one (Z-1-4). Liu *et al.* [42] reported an increase in electrolyte leakage in leaves of *Avena nuda* L. (naked oats) seedlings with cold stress and with prolongation of the stress period. LT stress leads to the destruction of cell membrane structure in maize plants [45], which caused increased permeability of membranes, and increased leakage of cell electrolytes and thus causing damage to plants. Electrolyte leakage was significantly (CD at 5%) lower in acclimated seedlings under LT stress, which probably suggested that membranes of acclimated seedlings were less affected under LT stress. Gong *et al.* [69] reported that electrolyte leakage from root tips of non-acclimated maize seedlings significantly increased after exposure to chilling stress, while cold shock pre-treatment remarkably reduced the leakage of electrolytes under chilling stress as compared to non-acclimated. Aaron *et al.* [168] reported that cold acclimation enhanced the freezing tolerance in *Petunia hybrida* and decreased the EL₅₀ value. In conclusion, acclimation prior to LT stress results in the enhanced tolerance of plants. Different types of molecules accumulate under stress conditions, which are used as a potential acclimatizing agent for plants in the form of a spray.

8. Conclusion

The LT stress negatively impacts the plant's performance, and survival percentage, through the generation of ROS. ROS accumulate under the stress in plants from different cell organelles. To deplete these ROS plants, activate the defense system, which includes enzymatic and nonenzymatic antioxidants. These together are involved in the detoxification of the accumulated ROS and enhance resilience against cold stress. Carbohydrates, proteins, and phenolic compounds also accumulate under stress conditions, helping in scavenging the ROS species. Acclimation is a method in which the plants are allowed to be exposed under nonfreezing and non-injurious temperatures, which leads to certain changes in plants that confer subsequent tolerance to cold injury.

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