Journal of Physical, Biomedical and Biological Sciences
eISSN: 3005-6489
www.jpbab.com
*J. Phys. Biomed. Biol. Sci., 2025; Volume, **4**: 43*

Review Article **Open Access**

BIOCHEMICAL, PHYSIOLOGICAL AND MOLECULAR RESPONSES OF THE HORTICULTURAL CROPS TO COLD RESPONSES

TAHIR A[1*], ASHRAF M[2], SHABIR F[1]

[1]Department of Entomology, Faculty of Agricultural Sciences, University of the Punjab, P.O BOX. 54590, Lahore, Pakistan
[2]Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences, University of the Punjab, P.O BOX. 54590, Lahore, Pakistan
**Correspondence Author Email Address: ayeshatahir2070@gmail.com*

(Received, 1st February 2023, Accepted 10th March 2025, Published 25th March 2025)

Abstract *A variety of abiotic stresses can affect horticultural crops, with low temperature being the most critical state. The environment has a tremendous impact on the productivity or quality of these crops. The quality and durability of horticultural crops are negatively impacted by cold stress, which includes freezing temperatures (less than 0°C) and chilling temperatures (0–15°C). Additionally, it disrupts the plants' philological and biological processes, resulting in symptoms such as stem elongation inhibition, wilting, fruit drop, chlorosis, and inhibition of cell division. The vegetative and reproductive growth of horticultural crops, such as papaya, banana, and coffee plants is similarly impacted by low temperature (LT). Cold stress also significantly affects cellular alterations, and disturbances in chlorophyll, photosynthesis, or cell membranes. Ca^{2+} and K^{+} ions serve as vital for controlling stress responses. This review emphasizes methods for improving cold stress and maintaining yield quality through optimal temperature control, while also highlighting the biochemical, molecular, and physiological responses of horticulture crops to cold stress.*

Keywords: *Cold acclimation; physiological changes; Stress signaling pathways; optimum temperature; Biochemical changes; Molecular response; Membrane injury*

Introduction

The productivity and quality of horticultural crops are significantly impacted by cold stress, a common abiotic factor. Some surfaces of the earth are covered with ice, while various regions have temperatures that make it difficult for plants to grow and survive (Ramankutty et al., 2008). In these conditions, plants need certain defenses to survive at low temperatures (LT). Chilling stress (0–15 °C) and freezing stress (<0 °C) are two types of cold stress (Thomashow, 1999). Low temperature have one of two effects on plants: 1. Chilling stress, which happens when plants suffer damage without ice crystals forming inside their cells after being exposed to LT below 10-15°C for an extended length of time 2. Plants that experience freezing stress, which results in cell dryness and freezing damage, are subjected to temperatures lower than 0 degrees Celsius(Beck et al., 2007; Zhu et al., 2007). Cold stress is a very quantitative characteristic for altered metabolic pathways, cell compartments, and regulations of gene or plant growth (Hannah et al., 2005). To increase plant output and guarantee food security, it's critical to understand how various horticultural crops respond to cold stress. Cold stress can also stop the many processes within the crop. Flowers or leaves may suffer from chilling harm and cold stress. Cold stress affects growth, yield, and production. Low, High temperature or quality has a strong correlation with photosynthesis and respiration (Ferrante and Mariani, 2018; Kasuga et al., 1999; Mariani and Ferrante, 2017). Temperature is a big influence directly on plant growth. Every horticulture crop has its optimum temperature. Plant growth is directly related to their Optimum temperature (Malhotra, 2017). Some winter crops require exposure to low temperatures (3-7°C) for the initiation of flowering. This response is known as Vernalization. In Low temperatures physiological and biochemical processes stop and Molecular mechanisms also affect. Cold temperature is favorable for some plants but not for all. LTS-related biochemical, molecular, and physiological mechanisms in horticultural crops (Hasanuzzaman et al., 2013). Plant growth and development are influenced by LT, which alters physiological, biochemical, and molecular processes (Miura and Furumoto, 2013; Nishiyama, 1976). Horticultural crops need more attention. The development, reproduction, growth, or eventual yield of the plant are all impacted by any change in environmental conditions or abiotic elements like temperature. The major technique utilized to preserve the quality of harvested horticulture crops is temperature control. Abiotic stresses affect multiple processes in plants (Francini and Sebastiani, 2019). Low temperature stress (LTS) negatively impacts horticultural plants' reproductive and vegetative development, resulting in lower yields and worse-quality products (Goswami et al., 2022).

Extreme waterlogging is a result of meteorological changes including drought, cold waves, and excessive rainfall, among other things. Given climate change and global warming, it may seem paradoxical to think that the greenhouse effect may be to blame for cold waves. Strong rains after periods of extreme drought or seasonal changes that lead to a thermal imbalance, For example, winters with average temperatures 1-2°C higher than historical records, followed by periods of extremely low temperatures are examples of seasonal variations that have an impact on water regimes (Cohen et al., 2013; Kodra et al., 2011; Rosenzweig et al., 2001; Trouet et al., 2018).

Table 1. Overview of an ideal temperature range for horticultural species' vegetative and reproductive development in given

Horticultural crops	Scientific Names	Optimum temperature (°C)	Reference (s)
Grapevine	*Vitis vinifera*	10-35°C	(White et al., 2006)
Banana	*Musa spp*	20-30°C	(Ahmad et al., 2001)
Guava	*Psidium guajava*	23-28°C	(Haryanto et al., 2021)
Mango	*Mangifera indica*	24-27°C	(Mukherjee and Litz, 2009)
Pomelo	*Citrus maxima L.*	23-30°C	(Huang et al., 2021)
Rambutan	*Nephelium lappaceum*	25-35°C	(Vargas-Hernandez et al., 2017)
Jackfruit	*Artocarpus heterophyllus*	16-28°C	(Haq, 2006)
Coconut	*Cocos nucifera*	31-43°C	(Mauro and Garcia, 2019)
Citrus	*Citrus spp*	25-30°C	(Abobatta, 2019)
Mangosteen	*Garcinia*	25-35°C	(Osman and Milan, 2006)

Cold stress effect on Horticultural crop

Physiological responses

Chilling damage is a physiological condition that causes aberrant ripening, pitting, or browning, which has a detrimental impact on horticulture goods and shelf life (Chen et al., 2008). LT stress significantly affects the reproductive or vegetative growth of horticulture crops (Alonso et al., 1997). Horticultural crops (vegetables and fruits) contain appreciable amounts of nutrients including minerals, carbohydrates, dietary fiber, vitamins, antioxidants, and some other components that are present that are essential for human health (Bellavia et al., 2013). Crops in the horticultural industry suffer severe damage from frost or unforeseen temperature changes throughout the winter. Fruit that has a meager yield. Furthermore, papaya blooms may become female under cold, humid circumstances, leading to malformed fruits (Awada, 1958; Lin et al., 2016; Storey, 1969). Due to improperly low temperatures, papayas can cause burning skin and water-soaked meat (Zou et al., 2014). Banana fruits suffer chilling harm at temperatures below 13°C, showing pitting on the peel surface, irregular ripening, and scent loss (Guo et al., 2018). Low temperatures in coffee plants hinder vegetative growth, reduce photosynthesis, and result in regulatory maturity or subpar yield (Bauer et al., 1985). Because of the reduced photosynthetic rate caused by the low temperature, plant growth decreased (Criddle et al., 1988). Reduced root elongation and cortical damage are caused by LT (Harrington and Kihara, 1960). LT has a detrimental effect on the horticultural goods' quality, reducing their potential for economic success. Problems with the reproductive organs' structure and function are brought on by cold stress. Low temperature (LT) can prevent fertilization or cause seeds or fruit to ripen too early (Farooq et al., 2009).

Cellular Change

The plant's cell membrane serves as the main location of the freezing damage (Levitt, 1980; Steponkus, 1984).

Acute dehydration is caused by chilling in the membrane. The chilling stress reduces the photosynthesis efficiency of sensitive plants. According to several studies, the principal locations of freezing damage in plants are cell membrane networks (Levitt, 1980; Steponkus, 1984), or freeze-induced membrane is a significant factor in plant injury. Plant injury is mostly brought on by severe dehydration that cold causes (Steponkus, 1984, 1993). Since the extracellular fluids of the apoplectic region have a larger freezing point and a lower solute concentration than the intracellular fluid, ice production first begins in these fluids (Jan and Andrabi, 2009).

Because ice has a lower water potential than liquid, extracellular ice has a lower water potential than inside the cell, which results in dehydration. Changes in the composition of membrane liquid, anomalies in cellular function, electrolyte leakage, and membrane damage are indicators of low-temperature stress injury (Mahajan and Tuteja, 2005; Shin et al., 2018; Yadav, 2010).

Studies have found that some sensitive plants' photosynthetic performance is decreased by cold stress (Fariduddin et al., 2011; Yang et al., 2005). Under LTS, carbon reduction cycle or thylakoid ETS route barriers drastically altered photosynthesis. Reduced photosynthetic rate is caused by stomatal regulation of CO2 supply (Allen and Ort, 2001). Limitations in stomatal conductance caused by the death of guard cells as a result of the cold have an impact on dehydration. The protracted chilling time has altered the chloroplast's ultrastructure (Yang et al., 2005). There are two essential nutrients Potassium and Calcium to improve plant chilling tolerance. Numerous studies have shown that plasma membrane cation conductance, which is predominantly responsible for K+ efflux from plant cells, is the main cause of electrolyte leakage. Low K+ levels cause damage from photo-oxidation brought on by freezing or frost is exacerbated. Plant growth and yield are reduced Applying K+ in higher concentrations reduces the LTS injury in the crops for example potatoes as a result. High potassium concentrations inside the cells protect them alongside oxidative damage brought on by freezing or frost (Waraich et al., 2012). The use of K+ with a higher concentration may reduce LTS damage to crops like potatoes (Grewal and Singh, 1980). Vegetable seedlings and carnations, respectively (Hakerlerler et al., 1997; Kafkafi, 1990). A high K+ content was also observed, and stomatal conductance and transpiration rate were both decreased (Pradhan et al., 2017). Ca also controls how the body reacts to stress during the healing process after a cold injury and while adjusting to cold stress (Palta, 1990). Intercellular vacuoles, which are the source of Ca2+, cause stomatal closure when the amount of Ca2+ inside the cell rises. Stomata are closed under the influence of Ca2+ (Wilkinson et al., 2001). For LTS to recover, Ca2+ is required. Through the activation of the plasma membrane enzyme ATPase, it revitalizes damaged cells(Palta, 1990). Calcium also functions as Camodulin, which controls metabolic activity and aids in growth of the plants (Waraich et al., 2012).

Chlorophyll

Chlorophyll is the key element of the photosystem. In leaves that are actively developing, LTS suppresses chlorophyll (Glaszmann et al., 1990). Compared to cold-sensitive lines, cold-tolerant genotypes may deposit more chlorophyll under LTS (Pradhan et al., 2019). An alternate method to gauge the freezing chlorophyll fluorescence measures a leaf's ability to tolerate freezing damage and adapt to cold (Ehlert and Hincha, 2008). To determine the degree of photodamage at low temperatures in different crops such as Arabidopsis (Ehlert and Hincha, 2008). Soybean (Tambussi et al., 2004), and maize (Aroca et al., 2001). The use of the chlorophyll fluorescence method Chlorophyll fluorescence, according to (Maxwell and Johnson, 2000), indicates PS II reactions brought on by LTS. According to (Smillie, 1979), papaya's quantum efficiency varied between 0.42 in the winter and 0.72 in the summer, showing that LT decreased PS II activity. Fluorescence in strawberries also reflects changes to the photosynthetic apparatus, and LTS decreased the value of chlorophyll fluorescence (Zareei et al., 2021). Fv/Fm decrease during LTS also discovered by (Pradhan et al., 2019).

Photosynthesis

At low temperatures, the metabolic process slows down and sometimes pauses under a lot of pressure (Araújo et al., 2013). LT affects the photosynthesis process in fruit crops. All major components are reduced due to disruption under LTS, which also includes the carbon reduction cycle and thylakoid electron transport mechanism. Long-term cooling reduces the chloroplast's ultrastructure and thylakoid membrane's ability to capture light (Yang et al., 2005). Due to LT, the electron transport chain is too reduced, which results in an Imbalance in the photosynthetic action in the thylakoid membrane (Ruelland et al., 2009; Soitamo et al., 2008; Yun et al., 2010). When compared to control plants, plants of papaya subjected to a Low-Temperature regime of 20/10°C (day/night) showed a 57.96% decline in photosynthesis. Their level of tolerance was genotype-dependent decreasing. When compared to other genotypes, chilling-sensitive red lady papaya had a dramatic decline (Satyabrata et al., 2018). When compared to the control (15/5°C; day/night; 4 days) plants of papaya exposed to LT regime had a 15% lower rate of photosynthesis according to (Grau and Halloy, 1997).

Due to lower stomatal conductance LTS also reduces leaf gas exchange in fruit crops which results in the production of ROS. The genotype resistant to LTS can maintain high leaf water potential (Wilkinson et al., 2001).

Biochemical Responses

The organic percentage of the waste stream's cellulosic component is broken down as part of the biochemical process. This might contain certain food items (fruits and vegetables), paper goods, and landscaping plants. Low-temperature stress altered the biochemistry of several cellular components and processes. Modifications in membrane lipid content brought on by LTS (Janská et al., 2010). The crop plants may be harmed by the chemical and physical stressors (Mehdizadeh and Mushtaq, 2020). However, to maintain an eco-friendly environment with desired horticultural yield, rigorous management is necessary (Calabrese, 2014; Vargas-Hernandez et al., 2017).

Cell membrane

The main event in cold stress is membrane damage. The cell is shielded from harm by the cell membrane. It offers a stable environment for intercellular biological activity. The metabolic processes are impacted once the membranes break down as a result of cold stress, which results in ion linkage, inadequate energy, and an excess of reactive oxygen species (ROS). Cell death and membrane rupturing are the outcomes (Patel et al., 2016). Ultrastructure study revealed that low temperatures harmed the membrane's integrity and function, cell death, or surface pitting (Wang et al., 2019). In their physical condition at low temperatures, the membrane lipid composition manifests itself in many ways, and the high concentration of unsaturated fatty acids is advantageous for supporting membrane function as it should be (Mendoza, 2014). Cold stress causes cell membrane damage or affects it, changing the plasma membrane's makeup. Increase the quantity of unsaturated fatty acids in the plasma membrane to lessen LTS damage (Theocharis et al., 2012). These adjustments guard against LTS damage to chloroplast envelopes and the plasma membrane (Matteucci et al., 2011). Under LTS, the chloroplast membrane has a greater concentration of saturated fatty acids [Yokoi et al., 1998]. When lipid peroxidation agents are added in LTS, The phospholipid bilayer of the cell membrane's lipid order is disrupted, and holes start to appear. Proteins and DNA can be oxidatively damaged by reactive substances. Examples include reactive oxygen or nitrogen species (Alonso et al., 1997; Van der Paal et al., 2016).

LTS related proteins

Lipoproteins are among the several metabolites and metabolic processes that LTS impacts (Miura and Furumoto, 2013). Plant cells synthesize the necessary proteins under the LTS to preserve the security or integrity of plasma membranes, chloroplastic envelop, and other cellular membranes. There are four protein families: LTI (cold-regulated proteins), RAB (responsive to abscisic acid), LEA (late embryogenesis abundant), and HSPs (heat-shocked proteins). The most common LEA protein, dehydrins, maintains cell membrane stability when exposed to cold stress (Bies-Etheve et al., 2008; Sun et al., 2013). After cold accumulation in guava, (Hao et al., 2009) conducted studies of leaf proteins. It has also been found that plants under cold stress denaturate their proteins (Guy and Niemi). After some time, Pardhan discovered that papaya leaves that had undergone cold treatment had 35.51% more total protein (Pradhan et al., 2017).

Signaling and Molecular responses

Phytohormones

During abiotic stressors such as drought, cold, salt, light, and heavy metal stresses, abscisic acid, ethylene, jasmonic acid, and salicylic acid (SA) are essential because they serve as connections between the stress regulator and the reactions of cells, tissues, and organs to outside stimuli(Rachappanavar et al., 2022).

Molecular responses

Environmental stressors such as salinity and excesses in temperature are the primary causes of floral losses. It is a widespread issue that has a major effect on plant development, reduces crop quality, or even affects crop distribution across geographical areas. Through molecular networks, plants adapt to their surroundings (Wang et al., 2014). LT leads to biochemical changes and physiological in the plant cells e.g. membrane rigidification, decreased enzyme kinetic, metabolic instability, etc. Different plant species respond differently to cold stress and as a result, the metabolism of those plants is altered by redirecting the expression of various stress (Chinnusamy et al., 2010; Guo et al., 2018). Plant starts the chain of processes that lead to the expression of genes (Zuther et al., 2019) which in turn promotes biochemical and physical changes that increase their tolerance to subfreezing conditions Plants change the composition of the cell membrane, the translational state of the protein and ROS system as a part of their adaptive response to cold stress. Gene expression is necessary for these systems. Tropical and subtropical crops are vulnerable to cold stress, but temperature crops can adapt to it (Chinnusamy et al., 2010).

Conclusion

LTS affects nearly every aspect of cellular function as well as the quality of crop yield. LTS unfavorable affects the entire development and growth of the horticulture crops. However Researchers have thoroughly tested the understanding of low-temperature harm on several field crops. The physiological, molecular, and biochemical processes behind Low-temperature stress tolerance and resistance in fruit crops under open and simulated LT conditions require more study. This aids in genetic advancement and cultural practice standardization for the productive development of horticulture crops.

Reference

Abobatta, W. F. (2019). Influence of climate change on citrus growth and productivity (effect of temperature). *Adv. Agric. Technol. Plant Sci* **2**, 180036.

Ahmad, S., Thompson, A., Hafiz, I. A., and Asi, A. A. (2001). Effect of temperature on the ripening behavior and quality of banana fruit.

Allen, D. J., and Ort, D. R. (2001). Impacts of chilling temperatures on photosynthesis in warm-climate plants. *Trends in plant science* **6**, 36-42.

Alonso, A., Queiroz, C. S., and Magalhães, A. C. (1997). Chilling stress leads to increased cell membrane rigidity in roots of coffee (Coffea arabica L.) seedlings. *Biochimica et Biophysica Acta (BBA)-Biomembranes* **1323**, 75-84.

Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., and Chown, S. L. (2013). Heat freezes niche evolution. *Ecology letters* **16**, 1206-1219.

Aroca, R., Irigoyen, J. J., and Sánchez-Díaz, M. (2001). Photosynthetic characteristics and protective mechanisms against oxidative stress during chilling and subsequent recovery in two maize varieties differing in chilling sensitivity. *Plant Science* **161**, 719-726.

Awada, M. (1958). Relationships of minimum temperature and growth rate with sex expression of papaya plants (Carica papaya L.).

Bauer, H., Wierer, R., Hatheway, W., and Larcher, W. (1985). Photosynthesis of Coffea arabica after chilling. *Physiologia Plantarum* **64**, 449-454.

Beck, E. H., Fettig, S., Knake, C., Hartig, K., and Bhattarai, T. (2007). Specific and unspecific responses of plants to cold and drought stress. *Journal of biosciences* **32**, 501-510.

Bellavia, A., Larsson, S. C., Bottai, M., Wolk, A., and Orsini, N. (2013). Fruit and vegetable consumption and all-cause mortality: a dose-response analysis. *The American journal of clinical nutrition* **98**, 454-459.

Bies-Etheve, N., Gaubier-Comella, P., Debures, A., Lasserre, E., Jobet, E., Raynal, M., Cooke, R., and Delseny, M. (2008). Inventory, evolution and expression profiling diversity of the LEA (late embryogenesis abundant) protein gene family in Arabidopsis thaliana. *Plant molecular biology* **67**, 107-124.

Calabrese, E. J. (2014). Hormesis: from mainstream to therapy. *Journal of cell communication and signaling* **8**, 289-291.

Chen, J. y., He, L. h., Jiang, Y. m., Wang, Y., Joyce, D. C., Ji, Z. l., and Lu, W. j. (2008). Role of phenylalanine ammonia-lyase in heat pretreatment-induced chilling tolerance in banana fruit. *Physiologia Plantarum* **132**, 318-328.

Chinnusamy, V., Zhu, J.-K., and Sunkar, R. (2010). Gene regulation during cold stress acclimation in plants. *Plant stress tolerance: Methods and protocols*, 39-55.

Cohen, J., Jones, J., Furtado, J. C., and Tziperman, E. (2013). Warm Arctic, cold continents: A common pattern related to Arctic sea ice melt, snow advance, and extreme winter weather. *Oceanography* **26**, 150-160.

Criddle, R., Breidenbach, R., Lewis, E., Eatough, D., and Hansen, L. (1988). Effects of temperature and oxygen depletion on metabolic rates of tomato and carrot cell cultures and cuttings measured by calorimetry. *Plant, Cell & Environment* **11**, 695-701.

Ehlert, B., and Hincha, D. K. (2008). Chlorophyll fluorescence imaging accurately quantifies freezing damage and cold acclimation responses in Arabidopsis leaves. *Plant Methods* **4**, 1-7.

Fariduddin, Q., Yusuf, M., Chalkoo, S., Hayat, S., and Ahmad, A. (2011). 28-homobrassinolide improves growth and photosynthesis in Cucumis sativus L. through an enhanced antioxidant system in the presence of chilling stress. *Photosynthetica* **49**, 55-64.

Farooq, M., Aziz, T., Wahid, A., Lee, D.-J., and Siddique, K. H. (2009). Chilling tolerance in maize: agronomic and physiological approaches. *Crop and Pasture Science* **60**, 501-516.

Ferrante, A., and Mariani, L. (2018). Agronomic management for enhancing plant tolerance to abiotic stresses: High and low values of temperature, light intensity, and relative humidity. *Horticulturae* **4**, 21.

Francini, A., and Sebastiani, L. (2019). Abiotic stress effects on performance of horticultural crops. Vol. 5, pp. 67. MDPI.

Glaszmann, J.-C., Kaw, R., and Khush, G. S. (1990). Genetic divergence among cold tolerant rices (Oryza sativa L.). *Euphytica* **45**, 95-104.

Goswami, A. K., Maurya, N. K., Goswami, S., Bardhan, K., Singh, S. K., Prakash, J., Pradhan, S., Kumar, A., Chinnusamy, V., and Kumar, P. (2022). Physio-biochemical and molecular stress regulators and their crosstalk for low-temperature stress responses in fruit crops: A review. *Frontiers in Plant Science* **13**.

Grau, A., and Halloy, S. (1997). Effect of chilling on CO2 gas-exchange in Carica papaya L and Carica quercifolia (A. St. Hil.) solms. *Journal of plant physiology* **150**, 475-480.

Grewal, J., and Singh, S. (1980). Effect of potassium nutrition on frost damage and yield of potato plants on alluvial soils of the Punjab (India). *Plant and Soil* **57**, 105-110.

Guo, Y.-f., Zhang, Y.-l., Shan, W., Cai, Y.-j., Liang, S.-m., Chen, J.-y., Lu, W.-j., and Kuang, J.-f. (2018). Identification of two transcriptional activators MabZIP4/5 in controlling aroma biosynthetic genes during banana ripening. *Journal of agricultural and food chemistry* **66**, 6142-6150.

Guy, C., and Niemi, K. J. and Brambl, R. 1985 Altered gene expression during cold acclimation of spinach. *Proc, Natl. Acad. Sci. USA* **82**, 367393677.

Hakerlerler, H., Oktay, M., Eryüce, N., and Yagmur, B. (1997). Effect of potassium sources on the chilling tolerance of some vegetable seedlings grown in hotbeds. *Johnston, AE: Food Security in the WANA Region, The Essential Need for Balanced Fertilization. International Potash Institute, Switzerland*, 317-327.

Hannah, M. A., Heyer, A. G., and Hincha, D. K. (2005). A global survey of gene regulation during cold acclimation in Arabidopsis thaliana. *PLoS genetics* **1**, e26.

Hao, W., Arora, R., Yadav, A. K., and Joshee, N. (2009). Freezing tolerance and cold acclimation in guava (Psidium guajava L.). *HortScience* **44**, 1258-1266.

Haq, N. (2006). "Fruits for the Future 10: Jackfruit Artocarpus heterophyllus," Crops for the Future.

Harrington, J. F., and Kihara, G. M. (1960). Chilling injury of germinating muskmelon and pepper seed. *In* "Proceedings. American Society for Horticultural Science", Vol. 75, pp. 485-9.

Haryanto, H., Joni, K., Purnamasari, D. N., Rahmawati, D., Nahari, R. V., and Ibadillah, A. F. (2021). Initial Modeling for Smart Farming using Soil Temperature and Humidity. *In* "E3S Web of Conferences", Vol. 328, pp. 08004. EDP Sciences.

Hasanuzzaman, M., Nahar, K., Alam, M. M., Roychowdhury, R., and Fujita, M. (2013). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International journal of molecular sciences* **14**, 9643-9684.

Huang, X., Muneer, M. A., Li, J., Hou, W., Ma, C., Jiao, J., Cai, Y., Chen, X., Wu, L., and Zheng, C. (2021). Integrated nutrient management significantly improves Pomelo (Citrus grandis) root growth and nutrients uptake under acidic soil of southern China. *Agronomy* **11**, 1231.

Jan, N., and Andrabi, K. I. (2009). Cold resistance in plants: A mystery unresolved. *Electronic Journal of Biotechnology* **12**, 14-15.

Janská, A., Maršík, P., Zelenková, S., and Ovesná, J. (2010). Cold stress and acclimation–what is important for metabolic adjustment? *Plant Biology* **12**, 395-405.

Kafkafi, U. (1990). Impact of potassium in relieving plants from climatic and soil-induced stresses. *Johnston, AE: Food Security in the WANA Region, the Essential Need for Balanced Fertilization. International Potash Institute, Basel*, 317-327.

Kasuga, M., Liu, Q., Miura, S., Yamaguchi-Shinozaki, K., and Shinozaki, K. (1999). Improving plant drought, salt, and freezing tolerance by gene transfer of a single stress-inducible transcription factor. *Nature biotechnology* **17**, 287-291.

Kodra, E., Steinhaeuser, K., and Ganguly, A. R. (2011). Persisting cold extremes under 21st-century warming scenarios. *Geophysical research letters* **38**.

Levitt, J. (1980). "Responses of Plants to Environmental Stress, Volume 1: Chilling, Freezing, and High Temperature Stresses," Academic Press.

Lin, H., Liao, Z., Zhang, L., and Yu, Q. (2016). Transcriptome analysis of the male-to-hermaphrodite sex reversal induced by low temperature in papaya. *Tree genetics & genomes* **12**, 1-14.

Mahajan, S., and Tuteja, N. (2005). Cold, salinity and drought stresses: an overview. *Archives of biochemistry and biophysics* **444**, 139-158.

Malhotra, S. (2017). Horticultural crops and climate change: A review. *Indian Journal of Agricultural Sciences* **87**, 12-22.

Mariani, L., and Ferrante, A. (2017). Agronomic management for enhancing plant tolerance to abiotic stresses—drought, salinity, hypoxia, and lodging. *Horticulturae* **3**, 52.

Matteucci, M., D'angeli, S., Errico, S., Lamanna, R., Perrotta, G., and Altamura, M. (2011). Cold affects the transcription of fatty acid desaturases and oil quality in the fruit of Olea europaea L. genotypes with different cold hardiness. *Journal of experimental botany* **62**, 3403-3420.

Mauro, C. S. I., and Garcia, S. (2019). Coconut milk beverage fermented by Lactobacillus reuteri: optimization process and stability during refrigerated storage. *Journal of food science and technology* **56**, 854-864.

Maxwell, K., and Johnson, G. N. (2000). Chlorophyll fluorescence—a practical guide. *Journal of experimental botany* **51**, 659-668.

Mehdizadeh, M., and Mushtaq, W. (2020). Biological control of weeds by allelopathic compounds from different plants: a bioherbicide approach. *In* "Natural remedies for pest, disease and weed control", pp. 107-117. Elsevier.

Mendoza, D. d. (2014). Temperature sensing by membranes. *Annual review of microbiology* **68**, 101-116.

Miura, K., and Furumoto, T. (2013). Cold signaling and cold response in plants. *International journal of molecular sciences* **14**, 5312-5337.

Mukherjee, S., and Litz, R. E. (2009). Introduction: botany and importance. *In* "The mango: Botany, production and uses", pp. 1-18. CABI Wallingford UK.

Nishiyama, I. (1976). Male Sterility Caused by Cooling Treatment at the Young Microspore Stage in Rice Plants: XII. Classification of tapetal hypertrophy on the basis of ultrastructure. *Japanese Journal of Crop Science* **45**, 254-262.

Osman, M. B., and Milan, A. R. (2006). "Mangosteen: Garcinia mangostana L," University of Southampton, International Centre for Underutilised Crops.

Palta, J. P. (1990). Stress interactions at the cellular and membrane levels. *HortScience* **25**, 1377-1381.

Patel, B., Tandel, Y., Patel, A., and Patel, B. (2016). Chilling injury in tropical and subtropical fruits: A cold storage problem and its remedies: A review. *International Journal of Science, Environment and Technology* **5**, 1882-1887.

Pradhan, S., Goswami, A., Singh, S., Prakash, J., Goswami, S., Chinnusamy, V., Talukdar, A., and Maurya, N. (2019). Low temperature stress induced physiological and biochemical alterations in papaya genotypes. *South African Journal of Botany* **123**, 133-141.

Pradhan, S., Goswami, A., Singh, S., Prakash, J., Goswami, S., Chinnusamy, V., Talukdar, A., Srivastava, V., and Kumar, A. (2017). Physiological and biochemical alterations due to low temperature stress in papaya genotypes. *Indian Journal of Horticulture* **74**, 491-497.

Rachappanavar, V., Padiyal, A., Sharma, J. K., and Gupta, S. K. (2022). Plant hormone-mediated stress regulation responses in fruit crops-a review. *Scientia Horticulturae* **304**, 111302.

Ramankutty, N., Evan, A. T., Monfreda, C., and Foley, J. A. (2008). Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global biogeochemical cycles* **22**.

Rosenzweig, C., Iglesius, A., Yang, X.-B., Epstein, P. R., and Chivian, E. (2001). Climate change and extreme weather events-Implications for food production, plant diseases, and pests.

Ruelland, E., Vaultier, M.-N., Zachowski, A., and Hurry, V. (2009). Cold signalling and cold acclimation in plants. *Advances in botanical research* **49**, 35-150.

Satyabrata, P., Goswami, A., Singh, S., Jai, P., Suneha, G., Chinnusamy, V., Akshay, T., and Sharma, V. (2018). Growth, nutrient acquisition and physiological responses of papaya (Carica papaya) plants to controlled low temperature stress. *Indian Journal of Agricultural Sciences* **88**, 726-732.

Shin, H., Min, K., and Arora, R. (2018). Exogenous salicylic acid improves freezing tolerance of spinach (Spinacia oleracea L.) leaves. *Cryobiology* **81**, 192-200.

Smillie, R. M. (1979). The useful chloroplast: a new approach for investigating chilling stress in plants. *In* "Low temperature stress in crop plants", pp. 187-202. Elsevier.

Soitamo, A. J., Piippo, M., Allahverdiyeva, Y., Battchikova, N., and Aro, E.-M. (2008). Light has a specific role in modulating Arabidopsis gene expression at low temperature. *BMC plant biology* **8**, 1-20.

Steponkus, P. (1984). Role of plasma membrane in cold acclimation and freezing injury in plants. *Annu Rev Plant Physiol* **35**, 543-584.

Steponkus, P. (1993). A contrast of the cryostability of the plasma membrane of winter rye spiring oat-two species that widely differ in their freezing tolerance and plasma membrane lipid composition. *Advances in low-temperature biology* **2**, 211-312.

Storey, W. B. (1969). Pistillate papaya flower: a morphological anomaly. *Science* **163**, 401-405.

Sun, X., Rikkerink, E. H., Jones, W. T., and Uversky, V. N. (2013). Multifarious roles of intrinsic disorder in proteins illustrate its broad impact on plant biology. *The Plant Cell* **25**, 38-55.

Tambussi, E., Bartoli, C., Guiamet, J., Beltrano, J., and Araus, J. (2004). Oxidative stress and photodamage at low temperatures in soybean (Glycine max L. Merr.) leaves. *Plant Science* **167**, 19-26.

Theocharis, A., Clément, C., and Barka, E. A. (2012). Physiological and molecular changes in plants grown at low temperatures. *Planta* **235**, 1091-1105.

Thomashow, M. F. (1999). Plant cold acclimation: freezing tolerance genes and regulatory mechanisms. *Annual review of plant biology* **50**, 571-599.

Trouet, V., Babst, F., and Meko, M. (2018). Recent enhanced high-summer North Atlantic Jet variability emerges from three-century context. *Nature Communications* **9**, 180.

Van der Paal, J., Neyts, E. C., Verlackt, C. C., and Bogaerts, A. (2016). Effect of lipid peroxidation on membrane permeability of cancer and normal cells subjected to oxidative stress. *Chemical science* **7**, 489-498.

Vargas-Hernandez, M., Macias-Bobadilla, I., Guevara-Gonzalez, R. G., Romero-Gomez, S. d. J., Rico-Garcia, E., Ocampo-Velazquez, R. V., Alvarez-Arquieta, L. d. L., and Torres-Pacheco, I. (2017). Plant hormesis management with biostimulants of biotic origin in agriculture. *Frontiers in Plant Science* **8**, 1762.

Wang, J., Wang, Q., Yang, Y., Liu, X., Gu, J., Li, W., Ma, S., and Lu, Y. (2014). De novo assembly and characterization of stress transcriptome and regulatory networks under temperature, salt and hormone stresses in Lilium lancifolium. *Molecular biology reports* **41**, 8231-8245.

Wang, Y., Ji, S., Dai, H., Kong, X., Hao, J., Wang, S., Zhou, X., Zhao, Y., Wei, B., and Cheng, S. (2019). Changes in membrane lipid metabolism accompany pitting in blueberry during refrigeration and subsequent storage at room temperature. *Frontiers in Plant Science* **10**, 829.

Waraich, E., Ahmad, R., Halim, A., and Aziz, T. (2012). Alleviation of temperature stress by nutrient management in crop plants: a review. *Journal of soil science and plant nutrition* **12**, 221-244.

White, M. A., Diffenbaugh, N., Jones, G. V., Pal, J., and Giorgi, F. (2006). Extreme heat reduces and shifts United States premium wine production in the 21st century. *Proceedings of the National Academy of Sciences* **103**, 11217-11222.

Wilkinson, S., Clephan, A. L., and Davies, W. J. (2001). Rapid low temperature-induced stomatal closure occurs in cold-tolerant Commelina communis leaves but not in cold-sensitive tobacco leaves, via a mechanism that involves apoplastic calcium but not abscisic acid. *Plant Physiology* **126**, 1566-1578.

Yadav, S. (2010). Cold stress tolerance mechanisms in plants. A review. Agron Sustain Dev 30: 515–527.

Yang, M.-T., Chen, S.-L., Lin, C.-Y., and Chen, Y.-M. (2005). Chilling stress suppresses chloroplast development and nuclear gene expression in leaves of mung bean seedlings. *Planta* **221**, 374-385.

Yun, K.-Y., Park, M. R., Mohanty, B., Herath, V., Xu, F., Mauleon, R., Wijaya, E., Bajic, V. B., Bruskiewich, R., and de Los Reyes, B. G. (2010). Transcriptional regulatory network triggered by oxidative signals configures the early response mechanisms of japonica rice to chilling stress. *BMC plant biology* **10**, 1-29.

Zareei, E., Karami, F., Gholami, M., Ershadi, A., Avestan, S., Aryal, R., Gohari, G., and Farooq, M. (2021). Physiological and biochemical responses of strawberry crown and leaf tissues to freezing stress. *BMC plant biology* **21**, 1-17.

Zhu, J., Dong, C.-H., and Zhu, J.-K. (2007). Interplay between cold-responsive gene regulation, metabolism and RNA processing during plant cold acclimation. *Current opinion in plant biology* **10**, 290-295.

Zou, Y., Zhang, L., Rao, S., Zhu, X., Ye, L., Chen, W., and Li, X. (2014). The relationship between the expression of ethylene-related genes and papaya fruit ripening disorder caused by chilling injury. *PLoS One* **9**, e116002.

Zuther, E., Schaarschmidt, S., Fischer, A., Erban, A., Pagter, M., Mubeen, U., Giavalisco, P., Kopka, J., Sprenger, H., and Hincha, D. K. (2019). Molecular signatures associated with increased freezing tolerance due to low temperature memory in Arabidopsis. *Plant, Cell & Environment* **42**, 854-873.

Declaration

Acknowledgment

Not applicable.

Authors contribution

AT and MA wrote the initial draft of manuscript. FS, and MA collected the literature and wrote the manuscript, and edited the manuscript in original. All authors have read and approved the final manuscript. The author have read and approved the final manuscript.

Conflict of Interest

The authors state that there is no conflict of interests with regard to this study. There is no conflict of interest in any financial or personal manner concerning the development of this project, the gathering of data, the interpretation of the data, or the writing and publishing of this paper.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Data Availability statement

All authenticated data have been included in the manuscript.

Ethics approval and consent to participate

These aspects are not applicable in this paper.

Consent for publication

Not applicable