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Mechanisms of Chilling Injury and Technologies to Mitigate It in Mango Fruit: A Review

Hansika Sati[a], Sunil Pareek[a], Jeffrey K. Brecht[b], and Elhadi M. Yahia[c]

[a]Department of Agriculture and Environmental Sciences, National Institute of Food Technology Entrepreneurship and Management, Kundli, Sonepat, India; [b]Horticultural Sciences Department, University of Florida, Gainesville, Florida, USA; [c]Facultad de Ciencias Naturales, Universidad Autonoma de Queretaro, Queretaro, Mexico

ABSTRACT

Chilling injury (CI) is a major postharvest challenge in mango (*Mangifera indica*), leading to physiological and biochemical disruptions that reduce fruit quality. This review aims to provide a comprehensive understanding of CI progression, its underlying mechanisms, and effective mitigation strategies. It highlights key protective responses, including membrane stability, energy maintenance, antioxidant defense, and activation of chilling stress-responsive pathways like the gamma-aminobutyric acid shunt. The role of molecular regulators, such as C-repeat binding factors and the arginine and proline pathways, in CI tolerance is examined. Additionally, chemical (salicylic acid, jasmonic acid, melatonin, nitric oxide, progesterone, calcium lactate, sorbitol, polyol) and non-chemical (hot water, low-temperature conditioning, UV radiation, modified atmosphere packaging) treatments are studied for efficacy. The review emphasizes that optimizing these interventions can significantly mitigate CI symptoms, enhance fruit storability, and improve postharvest storage of mangoes.

KEYWORDS

Mangifera indica; low temperature; oxidation; physiological disorder; postharvest; storage; stress

Introduction

Mango (*Mangifera indica*), the king of fruits, is famous for its delicious taste, flavor, and nutritive value,[1] containing diverse nutrients, vitamins, organic acids, and fibers. Mango is also a rich source of other bioactive compounds such as phenolics and carotenoids. However, beyond physical damage concerns, mangoes are highly susceptible to chilling injury (CI) during cold storage, which leads to physiological disorders that affect fruit quality.[2] Proper postharvest handling, including optimal storage temperatures and careful transportation, is essential to prevent CI and ensure fruit marketability.[3] Prolonged exposure to temperatures below the chilling threshold can trigger CI symptoms. Specifically, CI in mangoes is characterized by surface pitting, sunken lesions, and internal browning, resulting from oxidative damage and increased membrane permeability. The disorder also disrupts volatile compound synthesis, leading to off-flavors and loss of aroma. In severe cases, the fruit's weakened structure makes it highly susceptible to microbial decay, further reducing marketability.[4] The globalization of trade has led to the expansion of transportation routes. The recent years have witnessed several developments in postharvest techniques to maintain mango shelf life. Among the methods available, the cold chain is the most effective means of maintaining the quality and extending the storability of mangoes.

However, as a chilling sensitive crop, low temperatures cannot be fully utilized to extend mango postharvest life. Prolonged storage of mangoes at temperatures below 9°C to 13°C (depending on maturity stage from half-ripe to mature green) leads to CI.[5] Maturity stage at harvest plays an

CONTACT Sunil Pareek sunil_ciah@yahoo.co.in Department of Agriculture and Environmental Sciences, National Institute of Food Technology Entrepreneurship and Management, Kundli, Sonepat, Haryana 131028, India

essential role in determining the fruit's susceptibility to CI. Mangoes harvested at the mature-green stage are the most venerable, as their cell walls and metabolic defenses are not fully developed to combat the chilling stress.[6] Partially ripe mangoes show moderate sensitivity, whereas half-ripe mangoes can tolerate temperatures around 10–12°C with lower damage. Fully ripe mangoes, though less affected by CI, are prone to rapid softening and quality loss, making precise temperature management essential for maintaining storage life while minimizing chilling damage.[7] Since mango is an important commercial commodity, CI has been proven to be responsible for significant economic loss in the market. Understanding and preventing the causes of CI in mangoes is, therefore, of major economic and scientific interest.[8]

Researchers have been committed to developing various postharvest treatments to mitigate the occurrence of CI in mangoes. Many chemical treatments, including salicylic acid (SA),[9] phenylalanine,[10] jasmonic acid (JA),[11] oxalic acid (OA),[12] melatonin (MT),[13–16] nitric oxide (NO),[17] sorbitol,[18] polyols,[19] and calcium lactate (CaLac),[20] and physical treatments including hot water treatment (HWT),[21] low-temperature conditioning (LTC),[22] ultraviolet (UV)-radiation,[23] controlled atmospheres (CA)[24–26] and modified atmosphere packaging (MAP),[27] intermittent warming (IW),[28] and cold-shock treatment,[29] have been found capable of mitigating CI in mangoes. To the best of our knowledge, a comprehensive literature dealing with technologies and mechanisms for mitigating CI in mangoes has yet to be reported. In this review, we summarize the proposed mechanisms behind the occurrence of CI in mangoes, in addition various physical, chemical methods, and molecular approach to mitigate mango CI are discussed. The review also discusses various mechanisms involved in CI alleviation and specific biochemical and physiological changes caused by CI in mangoes. Additionally, in this review, we provide suggestions of future research directions for avoiding and controlling CI in mangoes.

Methodology

To develop an understanding of the work done concerning CI in mango, based on the journal type and the source type, a total of 178 documents were identified from the Scopus database by using the keywords 'Mango' AND 'Chilling Injury', with filters applied to included peer-reviewed research article, conference papers, reviews, and book chapter. The publication range considered was 1995–2024, ensuring a comprehensive analysis of past and recent advancements in the field.

The sources included 124 journal articles, 47 conference papers, 3 reviews, and 4 book chapters. The VOS viewer technique was implemented to understand the bibliographic data extracted. For mapping, the minimum occurrence was set as 5, and the total keywords were selected. A total of 52 keywords (items) were identified, having 5 clusters and 797 links, with a total link strength of 2158. The term 'link' stands for the relationship between two items. A positive numerical value is used to denote the strength developed by each link; the higher this value, the stronger the link. A network visualization map was used to depict the above bibliographic data. In the network visualization, the items are represented by circles. The size of the circle determines the weight of the item. The network visualization map (Fig. 1) showed metabolism and temperature as the keywords most encountered. The circles having similar colors suggest similar topics among publications, each represents a subfield of the research on mangoes concerning CI.

Figure 1 has five clusters, each represented by a different color. Cluster 1 in red shows studies on mitigating CI in mango, considering factors like "oxidative stress" and "ion leakage". Cluster 2 in green links keywords related to postharvest management, like "respiration rate," "quality," and "storage life". These terms suggest that a significant body of research focuses on how CI impacts the overall storage quality of mangoes, respiration, and other physiological aspects of stored mangoes. Cluster 3 in dark blue emphasizes terms like "shelf life," "cold storage," and "food quality". This highlights research focused on the commercial impacts of CI and how storage techniques and treatments influence the shelf life and marketability of mangoes. The golden color represents cluster 4, which depicts studies focusing on antioxidant activity in mitigating mango CI. Lastly, cluster 5 denotes the effect on

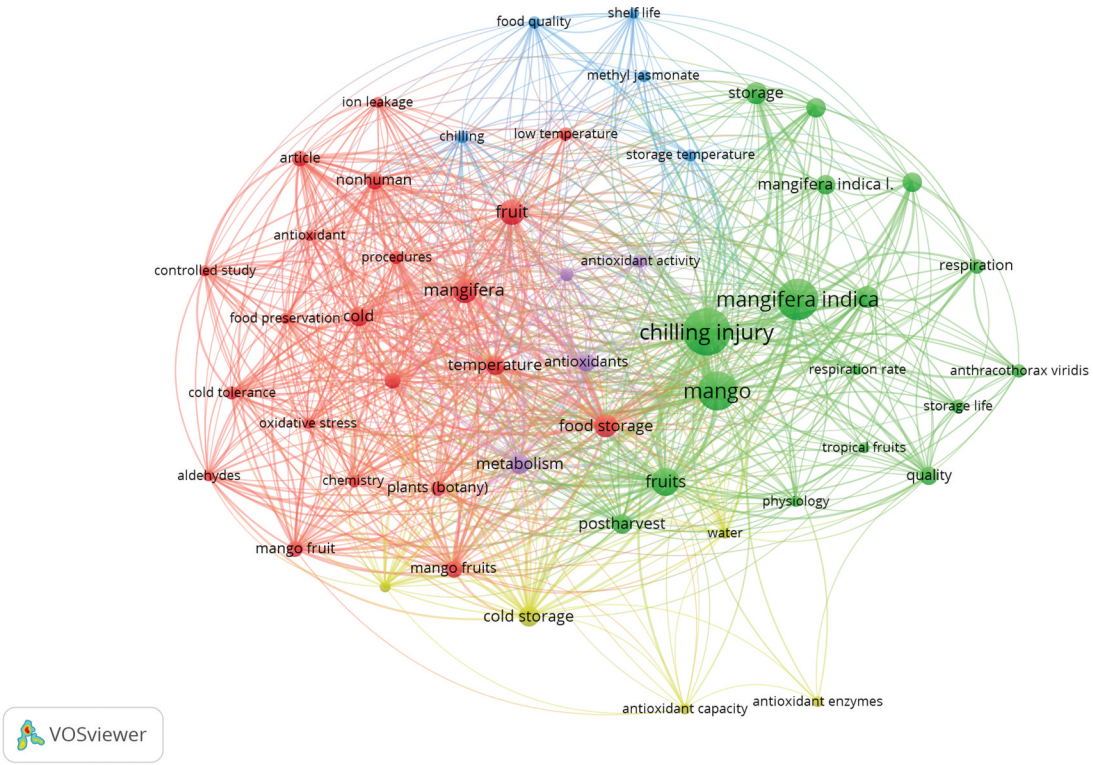

Figure 1. The VOS viewer software-based network visualization of total keywords co-occurrence in extracted papers related to chilling injury in mango from scopus database. The connecting lines between phrases show co-occurrences in the same article, and the keywords contained in the same cluster reveal that they have been analyzed frequently in the same publications.

metabolism in CI-affected mangoes. Using the above information obtained from Fig. 1, in this review we aimed to amalgamate the scattered work on mango CI. Additionally, this manuscript elucidates the mechanisms and discuss the physical and chemical methods and biochemical mechanisms that may be used to mitigate CI in mango.

Symptoms and natural progression of CI in mango

Membrane lipid transition theory

Lyons offered the first theory, which highlighted a membrane lipid phase transition into the gel phase lipids at a critical temperature. The conversion of the lipid phase into the gel phase due to low temperature led to disruption of membrane protein (enzyme) function and the leakage of cellular membrane contents, resulting in loss of compartmentation and integrity.[30] This transition ultimately results in an irreversible metabolic imbalance leading to plant death. Early evidence supporting this theory was based on plant mitochondrial studies. Chilling-resistant plants recorded a greater degree of lipid unsaturation than chilling-sensitive ones, which resulted in speculation of a relationship between chilling sensitivity and the physical structure of cellular membranes.[30,31]

Phases of CI development

The CI in mango occurs in two distinct phases. The first phase is a physical, temperature-dependent phase, which is also regarded to be a primary event. These are termed primary events, as the initiation starts as soon as the storage temperature drops below the threshold temperature for a prolonged

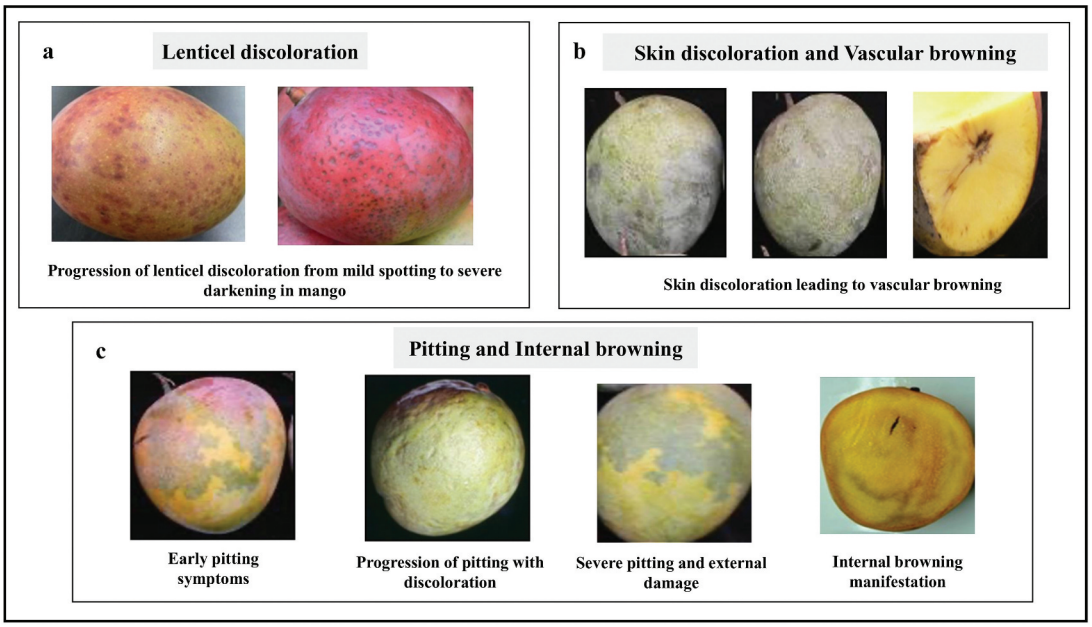

Figure 2. The figure denotes the progression of chilling injury in mango. a) Lenticel discoloration: initial symptom characterized by small, dark spots on the lenticels (pores) of the mango skin, b) skin discoloration and vascular browning: darkening of the skin and browning of the underlying vascular tissue, and c) pitting and internal browning: development of sunken areas (pits) on the skin, accompanied by internal browning and tissue breakdown.

duration. The metabolic dysfunctions caused by these primary events lead to certain secondary events. These secondary events depend upon the duration of time for which the fruit has been exposed to the chilling temperature.[32] CI is a physiological dysfunction that occurs in mangoes when they are exposed to a low temperature for a prolonged period; below 13°C.[13] The critical threshold temperature declines as mango fruit ripen.[33]

Characteristic symptoms of CI in mango

Appearance of CI symptoms in mango fruit follows a characteristic, sequential pattern.[34] The CI development in mango starts with the loss of aroma, which may never be recovered. These changes are associated with triggering enzymatic activity on exposure to cold temperatures.[35] The second stage of CI in mango is marked by lenticel discoloration, considered to be the earliest visual symptom (Fig. 2a). The onset of CI in mango affects the cell membrane integrity, including the cells around the lenticels. The enhanced phenolic content to scavenge reactive oxygen species (ROS) may accumulate around the lenticels and lead to lenticel discoloration.[36] Uneven ripening or inhibition of ripening upon return to ambient temperature from chilling temperature is a common chilling injury symptom in mango. The chilling temperature results in suppression of ethylene biosynthesis which persists upon transfer to warmer temperatures.[37] Further CI development leads to skin discoloration (Fig. 2b).[8]

Storing mango fruit at low temperatures may lead to fruit fermentation, which forms alcohols and aldehydes, marked by a gray or brown appearance followed by vascular browning. When the fruit is removed from cold storage and kept at room temperature for one to 2 days, the CI symptoms become more prominent and visible.[38] Further, mesocarp cell disruption and inhibition in the development of carotenoid pigments occur when the mangoes are stored at 7°C,[39] followed by the last stage of CI symptoms, which occur in mangoes as scald-like skin collapse, pitting, and internal mesocarp (flesh) browning (Fig. 2c).[40]

Histological aspects involved in mango CI

The CI in mangoes results in a variety of histological changes at the cellular and tissue levels, significantly impacting fruit quality and shelf life.[41] At the cellular level, subjecting to chilling temperatures results in phase transitions in lipid membranes, where the fluidity of the phospholipid bilayer is compromised, changing from liquid crystalline to a gel state. This shift weakens the membrane structure, leading to an inflexible and leakage-prone intracellular contents. This loss of membrane integrity is a primary CI indicator, and is frequently measured by electrolyte leakage assays, which exhibit comparatively higher ion influx in CI-affected mangoes than normal mangoes.[42] This enhanced permeability results in unrestricted exchange of solutes, hampering cellular homeostasis and enhanced tissue senescence. Additionally, alterations in membrane lipid composition, especially a reduction in the levels of unsaturated fatty acids, have been linked with increased chilling sensitivity.[43]

Plasmolysis is another significant histological alteration seen in CI-affected mangoes, where the plasma membrane separates from the cell wall due to excessive water loss and osmotic imbalance. This separation causes cellular shrinkage, deformation, and collapse.[44] Microscopic examination involving differential staining methods have displayed CI-affected cells to show plasmolysis, asymmetrical cell shapes, and a disintegrated middle lamella, which supplements accelerated tissue breakdown. Additionally, scanning electron microscopy (SEM) of chilled mango mesocarp has exhibited disintegrated cytoplasm with vacuolar shrinkage, disrupted cellular compartmentation, and abnormal aggregation of cellular components, further depicting irreversible chilling-associated damage.[45]

At the tissue level, CI affects both the epidermal and sub-epidermal layers of mango fruit, developing CI symptoms, including pitting, browning, and lenticel discoloration. The epidermis encounters multiple structural modifications due to chilling-induced cellular dehydration, leading to collapse of epidermal cells and cuticular degradation.[45] Transmission electron microscopy (TEM) studies have revealed the epidermal cells CI-affected mango to show disorganized cuticle layers, loss of cell turgor, and irregular accumulation of phenolic compounds, leading to skin browning. The deposition of oxidized polyphenols, especially around lenticels, has been associated with enhanced oxidative stress, as CI-induced ROS disrupt cellular redox balance.[46] The polymerization of these oxidized polyphenols leads melanin formation, causing peel discoloration. The lenticels, being natural epidermal openings, are particularly chilling sensitive and their discoloration is an early CI symptom, suggesting oxidative damage to be not only a secondary response but also a primary event in CI progression.

In addition to membrane instability and oxidative stress, cell wall degradation performs an important part in the histological aspect of CI. The CI disrupts the metabolism of structural polysaccharides, resulting in cell wall loosening and fruit softening. The enzymatic activity of pectin methylesterases (PME) and polygalacturonase is altered under chilling stress. An increased enzymatic activity of polygalacturonase in CI-affected mangoes corresponds with uncontrolled pectin solubilization, leading to weakened intracellular adhesion and enhanced fruit susceptibility to damage.[47] Histochemical staining of CI-affected mango mesocarp has confirmed the pectin degradation,[48] while SEM imaging has shown cell wall disintegration, further contributing to enzyme disruption is an essential factor in CI development.[49]

Mitochondrial dysfunction is another important histological outcome of CI, as ROS accumulation hampers cellular respiration and energy metabolism.[50] Studies on mitochondria of CI-affected mangoes show reduced enzymatic activity of cytochrome c oxidase and succinate dehydrogenase, denoting the impaired electron transport chain role. This causes lower ATP and enhanced ROS generation, causing a feedback loop of oxidative stress that accelerates cellular degradation. Chloroplasts, although less in number in mature mango mesocarp, also experience structural disruption under CI, resulting in loss of chlorophyll and carotenoid pigments, leading to color loss in CI-affected mangoes.[51] The final stage is marked by excessive cellular lysis and microbial invasion, severely affecting the marketability and fruit storage.[41]

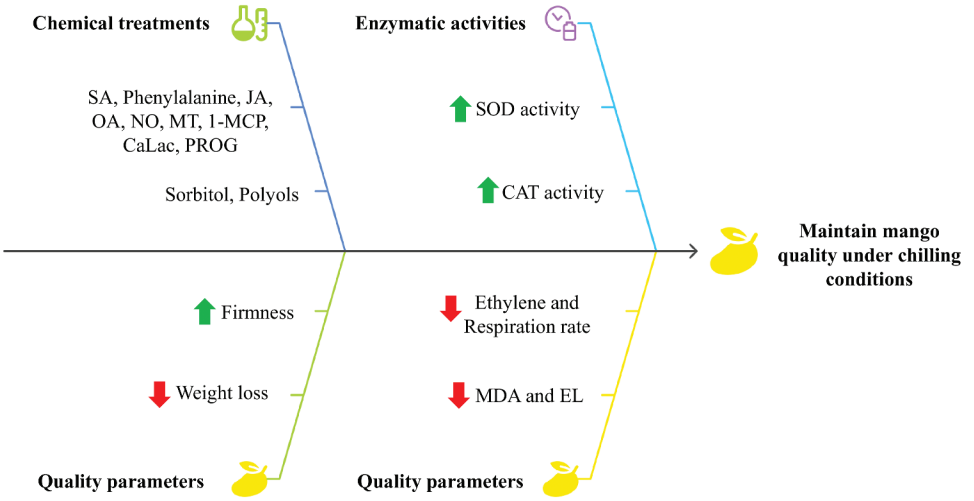

Figure 3. Schematic representation of the role of chemical treatments in maintaining mango quality under chilling conditions. Treatments like SA, JA, OA, NO, MT, 1-MCP, CaLac, and PROG enhance SOD and CAT activity, reducing oxidative stress. This leads to improved firmness, reduced weight loss, and lower ethylene, respiration rate, MDA, and EL, ultimately mitigating chilling injury. 1-MCP: 1-methylcyclopropene, CaLac: calcium lactate, CAT: catalase, EL: electrolyte leakage, JA: jasmonic acid, MDA: malondialdehyde, MT: melatonin, NO: nitric oxide, OA: oxalic acid, PROG: proline, SA: salicylic acid, SOD: superoxide dismutase.

Postharvest treatments to mitigate CI in mango

As CI leads to economic losses, several chemical and physical postharvest treatments have been developed for its mitigation. Chemical treatments like SA, phenylalanine, JA, OA, MT, NO, 1-methylcyclopropene (1-MCP), sorbitol, polyols, and CaLac have been reported to mitigate CI (Fig. 3; Table 1). Physical treatments like HWT, LTC, UV-radiation, CA storage, MAP, IW, and cold shock treatment also alleviate the incidence of CI in mangoes (Fig. 4; Table 2).

Chemical treatments

Salicylic acid (SA)

SA is a well-known endogenous plant growth regulator that has been documented to possess ROS scavenging capability. Treatment with 1 mm SA before storage at 5 ± 1°C and 90 ± 2% relative humidity (RH) for 42 d, effectively delayed CI in 'Nam Dok Mai' mango by 70–80% compared to the control. SA-treated mangoes had higher activities of ascorbate peroxidase (APX), catalase (CAT), and superoxide dismutase (SOD), which led to reduction of both ROS and the development of CI symptoms.[9] Reduced ROS led to lower malondialdehyde (MDA) content, thus lower membrane degradation. Higher non-enzymatic antioxidant activity was marked in SA-treated mango due to elevated levels of phenols and glutathione by activating the key enzyme for phenol biosynthesis, phenylalanine ammonia-lyase (PAL).[9]

Application of 2 mm SA to the 'Chausa' mango variety stored for 30 d at 8 ± 0.5°C and 90 ± 5% RH significantly mitigated the CI symptoms.[17] Higher amounts of bioactive compounds like phenols and carotenoids increased the antioxidant activity. 'Zill' mangoes, when treated with 2 mm SA and stored for 35 d at 5°C and 95% RH, exhibited lower O^{2-} content, indicating increased ROS scavenging activities.[52] Increased SOD activity was reported in SA-treated mango on storage days 15 and 25. CAT activity was found to increase in SA-treated mango from the 10th day onwards. Decreased O^{2-} content and increased CAT and SOD activity together contributed to reduced CI development. Reduced ROS contributed to lower lipid peroxidation and increased fruit firmness.[52]

Table 1. Effects of different chemical treatments in inducing chilling tolerance of mango fruits.

Type of chemical treatment	Mango variety	Dose (μM)	Storage temperature/ conditions	Effect on treated fruit w.r.t control	References
Salicylic acid	'Nam Dok Mai'	1000	5 ± 1°C, 90 ± 2% RH, 42 d	CII ↓ by 80% O_2 ↓ by 41% H_2O_2 ↓ by 51% SOD ↑ by 176% CAT ↑ by 110% APX ↑ by 140%	[9]
	'Chausa'	2000	8 ± 0.5°C, 90 ± 5% RH, 30 d	WL ↓ by 15.35% Firmness ↑ by 40% CII lower by 24% Respiration rate ↓ by 1.3-folds Ethylene formation ↓ by 32% Phenolics ↑ by 27% AOX ↑ by 47%	[17]
	'Zill'	2000	5°C, 95% RH, 35 d	O_2 ↓ by 38.46% H_2O_2 ↓ by 15.38% CAT ↑ by 22.22% APX ↑ by 15.38% MDA ↓ by 8% CII ↓ by 25%	[52]
Phenylalanine	'Shelly'	8000	7°C, 21 d	CII ↓ by 26.67% Firmness ↑ by 20% TSS ↑ by 11.76% Phenolics ↑ by 13.33% H_2O_2 ↓ by 37.78% CAT ↑ by 20% APX ↑ by 12.5% MDA ↓ by 13.04%	[5]
Jasmonic acid	'Kent'	100	5°C, 85–88% RH, 21 d	WL% ↓ by 12.5% Firmness ↑ by 27.27% CII ↓ by 81%	[11]
	'Tommy Atkins'	100	7°C, 21 d	CII ↓ by 2 folds EL ↓ by 20.83% Respiration rate ↓ by 40% WL% ↓ by 20.45%	[53]
Oxalic acid	'Zill'	5000	10 ± 0.5°C, 49 d	CII ↓ by 34.62% Firmness ↑ by 12% TA ↓ by 36.36% Proline ↑ by 6% ATP ↑ by 17.39% AMP ↓ by 10%	[54]
Melatonin	'Guifei'	500	4 ± 1°C, 85 ± 5% RH, 40 d	CII ↓ by 28.9%	[42]
	'Dashehari'	100	5 ± 1°C, 85–90% RH, 28d	CII ↓ by 3-folds MDA ↓ by 3.3-folds Respiration rate ↓ by 42.87% Ethylene formation ↓ by 30% WL% ↓ by 7.9% SOD ↑ by 60% CAT ↑ by 80%	[15]
	'Langra'	100	5 ± 1°C, 85–90% RH, 28d	CII ↓ by 3.5-folds Firmness ↑ by 28.57% ATPase ↑ by 50% Peel Exo-PG ↑ by 19.23% Pulp Exo-PG ↑ by 28.57%	[13]
	'Gulab Jamun'	100	5 ± 1°C, 85–90% RH, 28d	CII lower by 14.29% Firmness ↑ by 5% Peel Exo-PG ↑ by 1.23% Pulp Exo-PG ↑ by 16.67%	[13]

(*Continued*)

Table 1. (Continued).

Type of chemical treatment	Mango variety	Dose (μM)	Storage temperature/ conditions	Effect on treated fruit w.r.t control	References
Nitric oxide	'Chausa'	1000	8 ± 0.5°C, 90 ± 5% RH, 30 d	CII ↓ by 1.7-folds EL ↓ by 41% Respiration rate ↓ by 59% Ethylene production ↓ by 120% Firmness ↑ by 43% WL% ↓ by 46% PME ↓ by 81% PG ↓ by 30%	[55]
	'Kensington Pride'	10	5 ± 1°C, 93.9 ± 2.1% RH, 28 d	CII ↓ by 25% Ethylene production lower by 1.66-folds Respiration rate ↓ by 16.1%	[56]
	'Kensington Pride'	20	5 ± 1°C, 93.9 ± 2.1% RH, 28 d	CII lower by 35.14% Ethylene production ↓ by 2.13-folds Respiration rate ↓ by 18.1%	[56]
	'Kensington Pride'	40	5 ± 1°C, 93.9 ± 2.1% RH, 28 d	CII lower by 56.25% Ethylene production lower by 3.18-folds Respiration rate ↓ by 20.8%	[56]
1-methylcyclopropene	'Irwin'	5	10°C, 32 d	Firmness ↑ by 29.03% WL% ↓ by 37.5% EL ↓ by 57.69%	[57]
Polyols	'Palmer'	2.5%	8 ± 1°C, 75 ± 3.0% RH, 28 d	CII ↓ by 8.57% WL% ↓ by 14.06% H_2O_2 ↓ by 23.08% PPO ↓ by 25% CAT ↑ by 14.29% SOD ↑ by 25% APX ↑ by 36.17% MDA ↓ by 23.08%	[19]
Calcium lactate	'Keitt'	0.5%	5°C, 20 d	CII ↓ by 30.4% EL ↓ by 1.09-folds Antioxidant activity ↑ by 1.46-folds	[20]

CII = Chilling injury index; SOD = Superoxide dismutase; CAT = Catalase; APX = Ascorbate peroxidase; WL = Weight loss; AOX = Alternative oxidase; EL = Electrolyte leakage; MDA = Malondialdehyde; TA = Titratable acidity; PPO= Polyphenol oxidase; PME = Pectin methylesterases; PG = Peptidoglycan; ATP = Adenosine triphosphate; AMP= Adenosine monophosphate.

Phenylalanine

The phenylpropanoid pathway contributes to providing tolerance against plant stress conditions by generating flavonoids and anthocyanin.[10] Postharvest phenylalanine treatment to 'Shelly' mangoes reduced the CI symptoms like pitting (damaged lenticels), black spots, stem end rot, electrolyte leakage (EL), and fruit decay. The suppression of these symptoms was attributed to the induction of brassinosteroids and auxins, which are correlated with the phenylpropanoid pathway. That pathway is responsible for enhancing flavonoid content and increasing antioxidant activity, thus lowering lipid peroxidation. Lower lipid peroxidation levels decreased fatty acid degradation and aldehyde accumulation, which preserves mango aroma.[10]

The enhancement of the antioxidant system by phenylalanine helps scavenge excess ROS, and an increased ROS scavenging reduced hydrogen peroxide (H_2O_2) levels in phenylalanine-treated 'Shelly' mango fruit.[5] A comparative study on phenylalanine-treated 'Choke Anan' and 'Nam Dok Mai' mangoes stored at 4°C for 30 d reported that peel browning was correlated with phenylalanine ammonia lyase enzyme activity but not with free phenolic acids.[64] This study documented that peel browning rather than pulp browning is responsible for limiting the postharvest life of cold-stored mangoes.

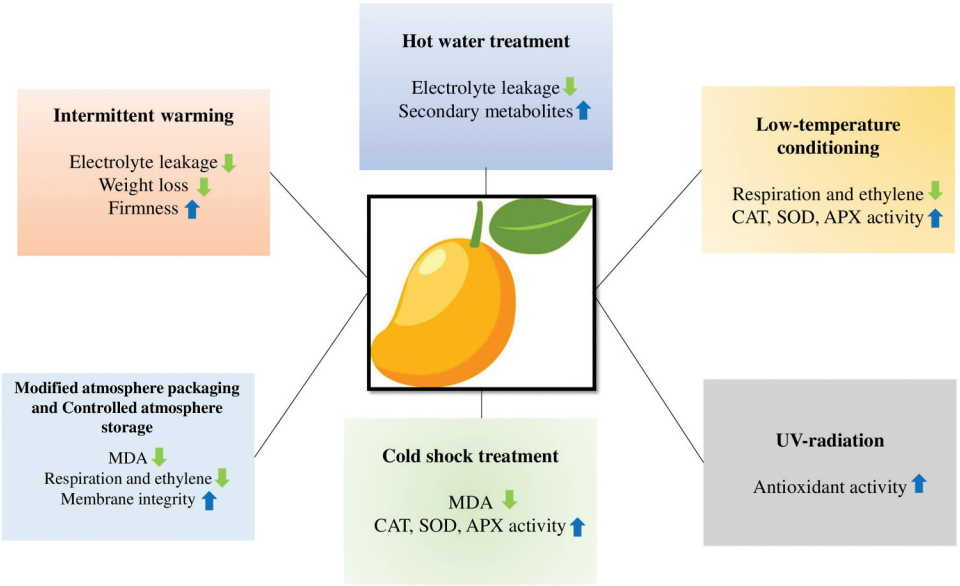

Figure 4. Effect of different physical treatments on mango fruit and schematic diagram of related mechanisms where the green arrow means down-regulation, the blue arrow means up-regulation, and the changes of indicators were compared to the control. SOD: superoxide dismutase, CAT: catalase, APX: ascorbate peroxidase, MDA: malondialdehyde.

Jasmonic acid (JA)

'Kent' mangoes stored at 5°C and 85–88% RH for 21 d that had been pretreated with JA vapors at 20°C for 20 h experienced good color development and reduced CI symptoms. Methyl jasmonate (MeJA) at 10^{-4} M proved to be the most effective concentration.[11] The MeJA lowered the mango's metabolic activity, leading to less acid breakdown and a higher total soluble solids (TSS) content. The treatment successfully maintained the fruit color. 'Tommy Atkins' mangoes treated with 10^{-4} M JA vapors for 24 h at 25°C and stored at 7°C for 21 d experienced an increased tolerance to chilling stress by increasing the levels of polyamines and ABA.[53] Treated mangoes were found to have a balanced ratio of unsaturated to saturated fatty acids, leading to decreased lipid peroxidation and EL and exhibiting better fruit quality.

Oxalic acid (OA)

Exogenous 5 mm OA to 'Zill' mangoes stored for 49 d at 10 ± 0.5°C resulted in lower CI symptoms.[54] The decreased CI symptoms were attributed to elevated proline levels in the peel and flesh due to increased Δ^1-pyrroline-5-carboxylate synthetase (P5CS) activity and decreased proline dehydrogenase (PDH) activity. These changes contributed to maintaining cellular osmolarity, stabilizing cellular structures, and higher adenosine triphosphate (ATP) concentration in the fruit flesh during storage. The treated fruit experienced reduced lipid peroxidation due to increased antioxidant capacity.[54]

A comparative study on 'Tommy Atkins' and 'Zill' mangoes reported that 'Tommy Atkins' showed CI symptoms externally including primary skin discoloration, while 'Zill' exhibited internal CI symptoms including flesh browning and gel formation.[12] When both cultivars were treated with 5 mm OA and stored at 10°C for 49 d, 'Zill' mangoes experienced lower CI symptoms. The lower occurrence of CI symptoms showed lesser damage to the plasma membrane. OA enhanced the enzymatic antioxidant activity by enhancing SOD, CAT, APX, and glutathione reductase (GR),[12] and these antioxidants acted as ROS scavengers and lowered H_2O_2 and O^{2-} levels. OA enhanced the enzymatic activity of succinate dehydrogenase (SDH), cytochrome-c-oxidase (CCO), H±ATPase, and

Table 2. Effects of different physical treatments in inducing chilling tolerance of mango fruits.

Type of physical treatment	Mango variety	Storage temperature/ conditions	Reported results	References
Hot water treatment	'Keitt'	HWT at 46.1°C, 90 min, storage at 5°C for 20 d	Lowered CI by enhancing the secondary metabolites, including gallic acid derivatives, and lowering electrolyte leakage	[21]
	'Keitt'	HWT at 46.1°C, 90 min, storage at 5°C for 20 d	Lowered CI by accumulating eleven heat shock proteins, eight energy metabolizing enzymes, and twenty-six proteins	[48]
	'Keitt'	HWT at 46.1°C, 90 min, storage at 5°C for 20 d	Lowered CI by accumulating osmolytes and phenolics, and increasing the antioxidant activity by maintaining the unsaturated/ saturated fatty acid ratio	[58]
Low-temperature conditioning	'Keitt' and 'Shelly'	Storage at 2°C, 19 d	Lowered CI by reduced ROS production	[22]
	'Guifei'	Keeping at 12°C for 24 h and stored at 5 ± 1°C, 85–90% RH, 25 d	Lowered CI by reducing MDA levels, and maintaining membrane integrity	[59]
UV-radiation	'Tommy Atkins'	46.1°C/90 min and 55°C/ 5 min followed by UV radiation doses of 1.14 kJ m^{-2} and 2.28 kJ m^{-2}, storage at 5°C for 14 d	Lowered CI by increasing the antioxidant activity	[23]
Controlled atmosphere storage	'Kensington'	10% CO_2, storage at 12°C	Lowered CI by decreasing the ethylene production	[60]
Modified atmosphere packaging	'Tommy Atkins' and 'Keitt'	Packed in 4-kg film-lined cartons by using microperforated polyethylene (PE) and Xtend film (XF) and stored for 21 d at 12°C	Lowered CI by decreasing the ethylene production and senescence	[60]
	'Samar Bahisht' 'Chaunsa'	Packed in Biofresh, Xtend, and Unbagged and stored for 35 days at 13 ± 1°C, 85–90% RH	Lowered CI by decreasing the ethylene production and senescence	[61]
	'Nam Dok Mai' 'See Tong'	Packed in polyethylene terephthalate box with perforated holes at a total area of 1.5 cm^2/ m^2 for 28 d	Lowered CI by decreasing the ethylene production and senescence	[27]
Intermittent warming	'Palmer' and 'Sensation'	1.0 mm MeJA + IW and storing at 5 ± 1°C for 15 d	Lowered CI by lowering lipid peroxidation, electrolyte leakage, and weight loss	[62]

(*Continued*)

Table 2. (Continued).

Type of physical treatment	Mango variety	Storage temperature/ conditions	Reported results	References
	'Keitt'	Packed in perforated polyethylene (PPE) bags and stored at or four days at 3 ± 1°C followed by three days of storage at 16 ± 1°C (IW), 13 ± 1°C, and 3 ± 1°C	Lowered CI by low H_2O_2 accumulation, better cell membrane intactness, and low weight loss	[28]
Cold shock treatment	'Naomi'	Coated with 3% alginate and 1% semperfresh, packed in edible coating with packing, and stored for 4 h at 0°C, followed by cold shock treatment at 20°C for 20 h, and were then stored at 2 ± 1°C, 90–95% RH, 15 d	Lowered CI by enhanced CAT, APX, and SOD activity	[29]
	'Wacheng'	Treatment at 0°C for 3, 4, or 5 h, and transferred to 20°C for 20 h followed by their storage for 12 d at 2°C, 85–95% RH	Lowered CI by enhanced CAT, APX, and SOD activity, which in turn decreased the MDA levels	[63]

CI = chilling injury; SOD = superoxide dismutase; CAT = catalase; APX = ascorbate peroxidase; MDA = malondialdehyde; APX = ascorbate peroxidase; ROS = reactive oxygen species; HWT = hot water treatment.

Ca^{2+}-ATPase, which helped in maintaining the ATP, adenosine diphosphate (ADP), and adenosine monophosphate (AMP) concentrations and thus preserving the energy status of the treated fruit.[12]

Melatonin (MT)

Exogenous treatment of 'Guifei' mangoes with 0.5 mmol L^{-1} MT resulted in lower MDA concentration, EL, and lipid peroxidation in response to MT treatment.[42] MT enhanced sphingolipid metabolism, which plays a critical role in stabilizing cell membranes and maintaining cellular integrity under stress conditions. By supporting membrane integrity and reducing lipid peroxidation, MT helped prevent the excessive loss of membrane fluidity, a hallmark of CI, thereby protecting the mango tissues from damage.

The activities of several lipid metabolizing enzymes like PLD, and lipoxygenase (LOX) were mitigated by MT.[42] Three different MT concentrations of 50, 100, or 150 µM were applied to 'Dashehari' fruit for 60, 90, or 120 min, respectively. The 100 µM MT concentration was the most effective, significantly reducing CI symptoms by lowering membrane lipid peroxidation, decreasing EL, and enhancing antioxidant enzyme activities, which collectively helped maintain membrane integrity and fruit quality during cold storage.[16]

A 100 µM MT treatment on 'Langra' stored at 5°C for 28 d caused lower CI symptoms.[15] It experienced lower degradation of endo-1,4-β-D-glucanase, endo, and exo-PG, which helped maintain cell wall integrity and delayed excessive fruit softening. This preservation of structural integrity is crucial for reducing CI, as it typically results in cell wall breakdown and tissue damage. Additionally, enzymatic activities of LOX and phospholipase D were found to decrease in the 'Langra' fruit, corresponding to an increased level of the linoleic, linolenic, and oleic acids, and lower amounts of stearic and palmitic acids, contributing to a higher unsaturated to saturated fatty acid ratio. Treatment with MT also elevated the enzymatic activity of succinate dehydrogenase, Ca^{2+}-ATPase, cytochrome c oxidase, and H^{+}-ATPase, leading to decreased APM and increased ATPA and ADP concentrations,

resulting in a higher adenylate energy charge (AEC).[15] Exogenous 100 µM MT application for 2 h on 'Chaunsa', 'Gulab Jamun', 'Langra', and 'Dashehari' mangos stored for 28 d at 5°C successfully delayed CI symptoms. It was reported in this study that MT successfully scavenged ROS, preventing H_2O_2 and O_2 accumulation, thus acting as an antioxidant.

MT elevated the levels of tyrosine ammonia lyase and phenylalanine ammonia-lyase in 'Dashehari' mangos, which increased the concentrations of total flavonoids and phenolic compounds.[15] The γ-aminobutyric acid (GABA) and endogenous polyamines accumulation in the peel and pulp of MT-treated 'Langra' mangos contributed to increased activity of ornithine decarboxylase (ODC), arginine decarboxylase (ADC), and lowered polyamine oxidase (PAO) and diamine oxidase (DAO) activities were documented to be the reason behind increased chilling tolerance.[13]

A study states MT to have anti-ethylene effects and properties in delaying fruit senescence.[65] A 200 µM MT with 1% tragacanth gum has been found to significantly maintain mango shelf-life by limiting ethylene production, modulating respiration rate, and lowering enzymatic degradation. The combination not only suppressed mango softening and weight loss but also maintained peel color, TSS, and phenolic content. Additionally, the combination regulated the fruit ripening enzymes, such as PME and polyphenol oxidase (PPO) better, thus showing slower degradation.[65] The combination proves to be an effective and promising postharvest strategy for commercial application in mitigating CI in mango.

Nitric oxide (NO)

As a multi-functional signaling molecule, NO is known to delay senescence in horticultural commodities, but has also been reported to influence CI.[66] Exogenous application of 1 mm NO to 'Chausa' mango stored for 30 d at 8 ± 0.5°C and 90 ± 5% RH, was found to lower CI incidence 1.5 to 1.7-folds by modulating key physiological processes associated with CI, including maintaining membrane integrity, lowering oxidative stress, and stabilizing cellular functions. Specifically, the rates of EL, an indicator of membrane damage was reported to be reduced by 26–41%. The rate of ethylene production also decreased by 117–120% compared to the fruit used as control, thereby reducing CI severity.[17]

Mangoes treated with NO exhibited 43% better firmness than those simply dipped in distilled water, which can be credited to NO's potential to mitigate CI by maintaining membrane integrity and protecting against cold-induced oxidative damage. This conservation of firmness is associated with lower enzymatic degradation of cell wall components, as NO treatments caused in 81% and 30% reductions in the activities of enzymes PME and peptidoglycan (PG), respectively. These enzymes typically activated under chilling stress, resulting in cell wall breakdown and tissue softening. Additionally, NO-treated mangoes experienced 46% lower weight loss, likely due to better preservation of cell membrane lipids, reducing EL and preventing chilling-induced water loss.[55]

A 5 µL L^{-1} NO application significantly lowered CI symptoms by maintaining fruit firmness and cellular stability for up to 2 d under low temperatures. At higher doses of 20 and 40 µL L^{-1}, NO could mitigate CI by lowering ethylene production and respiration rates, which are stress-induced responses linked to chilling damage. Additionally, NO reduced chlorophyll degeneration, a common symptom of CI, thereby helping to preserve the fruit's natural color. By modulating these stress responses, NO significantly protected mango fruit from the oxidative damage and membrane disruption typically associated with CI.[56]

1-methylcyclopropene (1-MCP)

1-MCP has been reported to mitigate CI in mango fruit by modulating ethylene responses, stabilizing membrane integrity, and increasing antioxidant activity. Studies have stated the efficacy of 1-MCP in alleviating CI symptoms and maintain mango quality under cold storage. A study on 'Irwin' mango found a 5 µL L^{-1} 1-MCP application significantly mitigated CI symptoms stored at 10°C for 32 d by limiting ethylene production, stabilizing membrane integrity, and delaying EL, an important indicator

of CI.[57] Additionally, 1-MCP-treated mangoes showed lower oxidative stress, resulting in better retention of fruit quality.

Another study on 'Tainong No. 1' mango stated 0.1 mg/L 1-MCP either alone or in combination with MT maintained postharvest quality of mango stored at 10°C for 25 d.[67] The treatment retained soluble sugars, ascorbic acid (AsA), and titratable acidity while minimizing color changes and repressing MDA accumulation, a marker of lipid peroxidation. The 1-MCP-treated mangoes showed enhanced activities of CAT, SOD, and APX, which supported lowered oxidative stress.[67] An even stronger regulatory effect on active metabolism was shown by the combination of 1-MCP and MT, indicating a synergistic effect in alleviating CI-induced metabolic disturbances.

These findings underscore the capability of 1-MCP in delaying ripening and mitigating CI. The efficacy of 1-MCP in maintaining membrane stability, lowering ROS accumulation, and hindering ethylene-responsive pathways makes it a beneficial postharvest tool for maintaining mango quality under cold storage.

Sorbitol and polyol

'Palmer' mangoes dipped in 2.5% (w/v) sorbitol and stored at 10°C for 32 d exhibited lower CI symptoms.[18] Lower CI was attributed to both enhanced enzymatic and non-enzymatic antioxidant defense activities. Sorbitol treatment boosted the activities of key antioxidant enzymes such as APX, CAT, and SOD, which contributed to improved enzymatic defense by effectively scavenging ROS. Additionally, non-enzymatic defenses were strengthened through elevated levels of polyphenols and vitamin C, which function as direct antioxidants. Together, these mechanisms helped reduce lipid peroxidation, as indicated by decreased MDA content, and lowered the oxidative stress associated with CI.[18] Polyols have been known to control viscosity and texture and reduce water activity. Treatment of 'Palmer' mangoes with polyols and storage at 8 ± 1°C and 75 ± 3.0% RH, for 28 d, developed less CI symptoms.[19] Polyol-treated mangoes experienced lower lipid peroxidation, which was associated with reduced accumulation of H_2O_2. The MT-treated fruit experienced higher SOD levels from 0 d onwards. It also affected the titratable acidity (TA), with higher concentration in the MT-treated fruit.[19]

Calcium lactate

A combination of HWT at 46.1°C for 75–90 min with 0.5% CaLac resulted in a 30.4% reduction in CI symptoms for 'Keitt' mangoes stored for 20 d at 5°C compared to the control. This treatment also led to a 1.09-fold reduction in EL compared to the control, indicating improved membrane stability. The increased calcium content contributed to stronger cell wall structure and maintained membrane integrity, which are important for mitigating CI and preserving fruit quality during cold storage.[20] Total phenolic compounds were higher in the treated mangoes. The antioxidant enzymatic activity of the treated fruit was 1.46 times more than the control. The combined HWT and CaLac increased the L-galacto-γ-lactone dehydrogenase activity, resulting in a higher AsA content in the treated fruit than in the control. CaLac improves cell wall firmness by enhancing the pectin linkages, maintaining cell turgor and membrane integrity, and preventing oxidation. Treated 'Keitt' mangoes also experienced higher carotenoids, indicating retention of normal ripening capacity despite the chilling storage temperature.[20]

In addition to this, a study found the effects of exogenous preharvest foliar CaLac on 'Keitt' mango, either alone or in combination with postharvest AsA or kojic acid.[68] The results showed that preharvest treatment of 2% CaLac significantly maintained harvest mango quality, while 2% CaLac along with postharvest 2% AsA was most successful in retaining key attributes, including fruit firmness, AsA, TSS, and total phenols. The study supports the effectiveness of the integrated exogenous preharvest CaLac and AsA.

Progesterone

Progesterone (PROG) application at an optimized concentration of 12 µM for 15 min effectively mitigate CI in mangoes stored at 6 ± 1°C for up to 4 weeks.[47] The PROG-treated mangoes showed a significant decline in EL and MDA accumulation. The CI progression hampers membrane lipid integrity, leading to enhanced EL and MDA levels due to lipid peroxidation. However, mangoes treated with PROG showed lower EL and MDA levels, indicating improved membrane stability and lower oxidative damage. The PROG treatment also suppressed the enzymatic activity of LOX, accountable for catalyzing the oxidation of polyunsaturated fatty acids. Exogenous PROG by lowering LOX activity aids in maintaining membrane fluidity, lowering CI-associated symptoms.[47]

Another important effect of PROG was its part in accelerating the mango antioxidant defense system. As CI progresses, it leads to excessive ROS production which results in cellular damage.[47] The application of PROG was successful in enhancing the enzymatic activity of SOD, CAT, and GR, which contributed in ROS neutralization. Additionally, mangoes treated with PROG were studied to have higher ATP and ATPase activity, signifying improved energy metabolism. The CI-affected mangoes face disrupted ATP generation which results in impaired cellular performance. The conservation of ATP levels assured sufficient energy supply for chilling stress adaptation; aiding mango tissues replenish their physiological integrity.

Beyond enhanced antioxidant activity and better membrane stability, PROG also modulated the activity of PME and PG. PME and PG are the pectin-modifying enzymes which govern cell wall remodeling, and their increased activity under cold storage resulted in rapid fruit softening.[47] Exogenous PROG regulated these enzymes which inhibited their excessive degradation and preserved the fruit firmness throughout cold storage.

Despite the widespread of SA, MT, NO, CaLac-based treatments, unpredictability in their efficacies stays a challenge, particularly due to application method, dosage sensitivity, and dissimilarities in fruit cultivar. Additionally, the capability of nano-formulations and interplay and genetic alterations may give deeper insights into how these applications regulate chilling-responsive genes in mango.

Non-chemical approaches

Hot water treatment (HWT)

When 'Keitt' mangos were treated with hot water at 46.1°C for 90 min followed by storage for 20 d at 5°C, the fruit peel experienced an accumulation of secondary metabolites. HWT alleviated CI symptoms and lowered the EL and MDA content. Expression of the genes encoding chalcone synthase (CHS), glucosyltransferase (UGT), and phenylalanine ammonium lyase (PAL) was enhanced in the HWT-treated fruit. Twenty metabolites, including benzoic acid derivatives, gallotannins, phaseic acid derivatives, gallic acid derivatives, and flavonoids, were identified in the hot water-treated mangoes. They exhibited higher antioxidant activity as measured by the ferric reducing ability of plasma (FRAP), 1,1-diphenyl-2-picrylhydrazyl (DPPH), and 3-ethylbenzothiazoline-6-sulfonic acid assays. Moreover, enhanced glutathione levels added to the enhanced antioxidant capacity of the hot water-treated mangoes.[21]

Similarly, HWT (46.1°C for 90 min) 'Keitt' mangoes stored for 20 d at 5°C were reported to have 26 differentially expressed proteins.[48] Enhanced polypeptide production in HWT mangoes was associated with up-regulation of 11 heat shock proteins (HSPs), specific secondary metabolites related to the enzymes PPO and PAL, three chloroplast metabolizing proteins (PDX1, rpl2, and RuBisCo), four antioxidant enzymes (CAT, APX, peroxidase, and peroxiredoxins), eight energy metabolizing enzymes, two proteins related to pathogenesis (2 s alb and β-Glu), and four cell wall metabolizing enzymes (αMan, β-Ga, EGase, and Rab11), which it was suggested helped in mitigating CI symptoms. Control mangoes exhibited higher PPO activity, denoting higher phenolic oxidation and lower energy production efficiency.[48]

In another study with 'Keitt' mangos treated with hot water at 46.1°C for 90 min, followed by storage at 5°C for 20 d, showed a delay in the loss of fruit firmness compared to the control and treated

fruit also retained higher soluble solids content, although pitting was observed in both control and treated fruit, but decay was only recorded in the control fruit.[58] HWT fruit maintained the ratio of unsaturated to saturated fatty acids. Thus, HWT helped maintain proper homeostasis. Gallotannin and alloylquinic acid levels were higher in HWT mangoes, imparting better cell wall stability. HWT of mangoes resulted in higher myoinositol levels, suggesting that inositol is a critical metabolite in combating chilling stress.[58] On the other hand, simple sugars like glucose, galactose, and fructose levels were found to be higher in HWT mangoes, which acted as a feed for the proper functioning of the oxidative pentose pathway, generating nicotinamide adenine dinucleotide phosphate (NADPH) and ATP, providing energy to HWT mangoes to mitigate chilling stress.[58]

Low temperature conditioning (LTC)

LTC is a technique that holds plant tissues sensitive to cold at temperatures above their recognized threshold values to induce chilling tolerance and has been documented to be an effective postharvest strategy to augment chilling stress tolerance and maintain mango quality.[59] A study on LTC 'Keitt' and 'Shelly' mangoes stored for 19 d at 2°C reported to have lower ROS production by down-regulating the linolenic acid pathway and lipid peroxidation, leading to lower CI symptoms.[22] LTC 'Guifei' mangoes at 12°C for 24 h and storage for 25 d at 5 ± 1°C and 85–90% RH had 42% lower development of CI symptoms than the control.[59] However, LTC accelerated fruit softening, with 21% more than the control mangoes, and except for the initial day, EL was decreased in LTC-treated mangoes. MDA levels exhibited a threefold increase in the control fruit that were kept at ambient temperature prior to chilling storage and MDA was found to be less in the treated fruit except on the first day. LTC mangoes possessed greater ROS scavenging activity, ensuring proper cell homeostasis and membrane integrity. Higher expression of the cold response gene *MiCBF1* was observed in the treated mangoes, which aided in providing chilling tolerance. These findings indicate that LTC collectively induced molecular and physiological responses and enhanced chilling tolerance.[59]

UV-radiation

Treatments utilizing UV-C radiation are considered to be among the most attractive methods for attenuating CI.[69] 'Tommy Atkins' mangoes stored at 5°C for 14 d were found to experience increased chilling tolerance when treated with hot water at 46.1°C for 90 min or 55°C for 5 min followed by UV radiation doses of 1.14 kJ m^{-2} or 2.28 kJ m^{-2}. Inhibition of CI symptom development is related to the enhanced antioxidant enzymatic activity of PAL and POD, and increased membrane integrity. UV-C radiation has the advantage of being a simple, dry, cost-effective, leaving no residues, making it fit for commercial use.[23] 'Tainong' mangoes kept at 10°C after being treated with a UV-B radiation dose of 5 kJ m^{-2} for 4 h experienced a reduction in CI symptoms and ion leakage levels. Low levels of MDA were observed, suggesting a properly maintained ratio of unsaturated fatty acids to saturated fatty acids after UV treatment, which may be helpful for maintaining membrane integrity.[70]

Controlled atmosphere storage (CA) and modified atmosphere packaging (MAP)

CA storage involves purposefully establishing, monitoring, and adjusting the levels of the respiratory gases O_2 and CO_2 in the storage environment. CA of 10% O_2 and 5% CO_2 effectively extended the shelf-life of 'Tommy Atkins' and 'Kent' mangoes, significantly reducing peel browning and pitting, the common symptoms of CI.[71] A CA of 10% CO_2 in air for 'Kensington' mangos stored at 12°C also alleviated CI symptoms. 'Kensington' mangoes stored at 12°C exhibited reduced red spot development around the lenticels (a CI symptom) and extended shelf-life.[60] A CA of 3% O_2 and 6% CO_2 has been reported to successfully extend the storage life of 'Kensington Pride' and 'R2E2' mango cultivars stored at 13°C by 6 weeks, a chilling treatment due to the extended exposure time. The mangoes had a higher concentration of aromatic volatile compounds, which was inhibited in the control fruit.[26]

In contrast to the tight control of CA, MAP involves the use of polymeric films to create an atmosphere different than air around the commodity, i.e., high CO_2 and low O_2. 'Tommy Atkins' and 'Keitt' mangoes packed in 4-kg film-lined cartons using microperforated polyethylene (PE)

and Xtend film (XF) and stored for 21 d at 12°C had less CI in XF packages compared to those of PE.[66] When 'Samar Bahisht Chaunsa' mangoes were packed in Biofresh, Xtend, or unbagged and stored for 35 d at 13 ± 1°C and 85–90% RH, the mangoes in Biofresh bags had the desired gas concentration, i.e., low O_2 and high CO_2, and exhibited a better visual appearance as they experienced lower CI and had better palatability than the mangoes in the other treatments.[61] A study of 'Nam Dok Mai See Tong' mangos stored for 28 d in a polyethylene terephthalate box with perforated holes with a total area of 1.5 cm^2/m^2 had no prominent CI symptoms and a longer shelf-life than air-stored fruit.[27]

Intermittent warming (IW)

The efficacy of IW combined with four different concentrations of MeJA was studied on 'Palmer' and 'Sensation' mangoes.[62] They found a treatment of 1.0 mm MeJA, combined with an IW regime that involved storing mangoes at 5 ± 1°C for 15 d, followed by 7 d at 20 ± 2°C, significantly alleviated CI symptoms. This IW treatment, when alternated with MeJA, minimized surface pitting, browning, and lesions. Additionally, it suppressed fruit weight loss, retained mango firmness, and maintained cell membrane integrity by preventing lipid peroxidation and reducing EL. The treatment enhanced the activities of antioxidant enzymes, including CAT, SOD, and APX, which contributed to better ROS scavenging activity and reducing oxidative stress.[62]

In another IW study, 'Keitt' mangoes packed in perforated polyethylene (PPE) bags (non-MAP) were exposed to different temperatures.[28] The mangoes were for a total of 56 d with 85–95% RH using three different storage temperature regimes: 1) a repeated sequence of 4 d at 3 ± 1°C followed by 3 d of storage at 16 ± 1°C (IW), 2) constant 13 ± 1°C, or 3) constant 3 ± 1°C. The IW-treated mangoes exhibited lower CI symptoms compared to constant low temperature storage. This was attributed to improved ROS scavenging, which reduced the accumulation of harmful H_2O_2, a major contributor to oxidative stress. Additionally, the IW treatment helped maintain cell membrane integrity by preventing lipid peroxidation, thus reducing EL and minimizing weight loss. These combined effects demonstrated how intermittent warming can mitigate chilling-induced damage and extend the shelf life of mangoes.[28]

Cold shock treatment

Cold-shock treatment involves rapidly exposing the mango fruit to a sudden drop in temperature, followed by a return to slightly warmer conditions, in an attempt to induce stress responses that build chilling tolerance.[72] Unlike low-temperature conditioning, which acclimates fruit gradually to colder temperatures, cold shock works by triggering rapid physiological reactions that can enhance antioxidant enzyme activities and strengthen the cell membrane, potentially reducing CI symptoms. 'Naomi' mangoes were coated with 3% sodium alginate and 1% Semperfresh, and packed in foam net to reduce CI during cold quarantine. The treated mangoes were initially stored at 0°C for 4 h as a cold-shock treatment, then transferred to 20°C for 20 h before being stored at 2 ± 1°C and 90–95% RH for 15 d. This cold shock treatment was found to mitigate CI, as mangoes subjected to the treatment resulted in a modest 5.7% reduction in CI symptoms compared to untreated mangoes. Additionally, these mangoes maintained better quality during storage.[29]

It was noted that the mangoes given cold shock treatment possessed better quality as they experienced a 5.7% lower CI than those without cold shock treatment. The untreated mangoes depicted a higher rate of respiration and ethylene production, leading to weight loss due to the loss of carbon atoms in the energy pathways. Loss of energy led to the degradation of the plasma membrane. Plasma damage resulted from enzymatic browning, which accumulated toxic substances and hampered the fruit's quality. A lower ripening rate in the treated mangoes protected the degradation of pectic compounds and maintained the fruit's firmness. Cold shock treatment enhanced the accumulation of phenolic compounds and CAT, APX, and SOD, which acted as potential antioxidants and provided the fruit with energy to combat the chilling stress.[29] Likewise, cold-

water shock at 0°C for 4 h prior to refrigeration of 'Wacheng' mangoes at 2°C was valuable in reducing CI symptoms by enhancing the antioxidant system.[63]

'Wacheng' mangoes treated at 0°C for 3, 4, or 5 h and, transferred to 20°C for 20 h, followed by their storage for 12 d at 2°C and 85–95% RH showed 70% less MDA compared to the control.[67] The treatment increased the levels of CAT, APX, and SOD, which were able to scavenge ROS and help in detoxifying the plant cell.[63] The ROS scavenging maintained the membrane integrity and cell homeostasis and induced a plant defense response that protected the plant against chilling stress and reduced CI symptom development. Cold shock treatment was also found to affect the ascorbate – reduced glutathione (GSH) pathway, which helped maintain the fruit quality by a continuous ROS scavenging activity.[63]

While non-chemical strategies like HWT, LTC, CA, and MAP have been studied, their effectiveness usually varies with mango cultivar and storage duration. An optimistic area for further research is the integration of several treatments, such as combining LTC with intermittent warming cycles to combat chilling stress. Additionally, harnessing the fruit microbiome through useful microbial coatings could provide an innovative approach, as recent studies indicate some endophytic bacteria mitigate chilling stress. Investigating real-time imaging and AI-based predictive models to analyze CI development could also lead to more accurate postharvest management strategies.

Mechanisms followed by different treatments for alleviating CI in mango

The primary strategy to preserve the postharvest quality of mango is keeping it in cold storage. Low temperature lowers the respiration rate and ethylene production, which delays ripening and senescence. However, storage at temperatures that are too low causes CI, which leads to undesirable losses in quality and contributes to economic losses. Alleviation of CI in mangoes can be achieved via various treatments. The success of these treatments in mitigating CI in mangoes may be attributed to 1) Maintaining membrane structure and energy status, which are compromised in CI; 2) Promoting the fruit's antioxidant system to overcome the increase in ROS that is inherent in CI; 3) Promoting the GABA shunt pathway to enhance the fruit's ability to respond to the stress of chilling temperature exposure; 4) Regulating arginine pathway and proline metabolism, also to enhance stress tolerance; and 5) Upregulating *CBF* genes to induce resistance to chilling stress.

Maintaining membrane structure and energy status

The reason behind CI is understood to be cell membrane damage, which sets in motion a cascade of secondary reactions, including interference with energy production and accumulation of certain toxic compounds. This involves interferences with energy production, resulting in a reduction in ATP availability. The lack of ATP and accumulation of ROS cause lipid peroxidation, compromising membrane fluidity and stability. This disruption leads to EL, increased respiration, and impaired cellular function, which are common CI symptoms in mango. These effects are primarily seen in the form of pitting, flesh browning, and increased susceptibility to decay. 'Zill' mangoes treated with OA were found to experience higher levels of ATP and energy charge from 28 d onwards during storage at 10 ± 0.5°C. Higher energy levels were documented to be the reason behind the better membrane integrity, lower lipid peroxidation, and reduced EL of the treated mangoes, which added to their enhanced chilling tolerance.[54]

The efficacy of MT has been studied in mango cvs. 'Langra' and 'Gulab Jamun'.[13] CI primarily affects membrane integrity, leading to a rise in EL and oxidative damage. MT-treated 'Langra' mangoes exhibited reduced membrane lipid peroxidation and increased membrane stability due to lower β-galactosidase and PG activities. This lowered the extent of cellular breakdown typically associated with CI. Additionally, MT accelerated the activities of H^+-ATPase, Ca^{2+}-ATPase, SDH, and CCO, leading to improved energy metabolism and maintenance of cellular function, which are essential in mitigating CI symptoms.[15]

'Zill' mangoes stored at 5°C exhibited typical CI symptoms under light microscopy, including abnormal cell wall separation at tricellular junctions and cell swelling, which are associated with membrane damage. However, mangoes treated with methyl salicylate (MeSA) showed no abnormal cell wall swelling, indicating that MeSA helped maintain cell structure and integrity under cold stress. MeSA inhibited CI by lowering the solubilization of pectin in the cell wall, thus preserving cell wall strength and minimizing EL with membrane degradation. Moreover, MeSA-treated mangoes showed higher levels of esterified pectins, which contributed to maintaining cell wall rigidity, while carboxylated pectins-often linked to cell wall degradation during CI, were reduced. The stabilization of the cell wall and the delayed accumulation of phenolics helped protect the mangoes from CI-related damage, resulting in better overall fruit quality during cold storage.[49]

Three types of treatments were given to 'Keitt' mangos, namely, quarantine HWT (46.1°C, 75–90 min), CaLac, 0.05%, and quarantine HWT + CaLac (0.05%), where the CaLac-treated mangoes experienced a lower EL (67.7%) when compared to the untreated mangoes, indicating better membrane integrity and lower CI-linked damage. Higher EL values in the control mangoes were linked to accelerated membrane disruption, which is a key symptom of CI, as cold temperature enhances membrane permeability. The imbalance in the unsaturated-to saturated fatty acid ratio in the cell membranes led to enhanced lipid peroxidation, a common outcome of chilling stress. This oxidative damage led to increased MDA levels, a stress marker of lipid peroxidation.[73]

The combination of HWT and CaLac efficiently lowered lipid peroxidation and stabilized membrane structures, safeguarding the mangoes from CI-related breakdown of membrane lipids. Mangoes treated with HWT+CaLac maintained firmness during cold-temperatures, likely due to higher cell membrane stability and reduced enzyme activity related to cell wall degradation. These treatments, by preserving membrane integrity and inhibiting oxidative damage, aided prolong the mangoes' shelf life and lowered the severity of CI symptoms during cold storage.[50]

Promoting the antioxidant system

Physical and chemical treatments can induce CI resistance after harvest by enhancing the antioxidant system (Fig. 5). Phenylalanine treatment of 'Shelly' mangoes enhanced the total flavonoids, total phenolics, and anthocyanins, all of which contribute to antioxidant capacity. The treatment also significantly enhanced DPPH scavenging activity, denoting improved ability to neutralize ROS.[5] Notably, phenylalanine treatment stimulated the production of a specific flavonoid and a kaempferol glycoside, both of which were linked to stronger ROS-scavenging properties in the mango fruit. Treated mangoes showed increased antioxidant activity, which helped mitigate the oxidative stress caused by ROS produced at chilling temperatures. By lowering the accumulation of H_2O_2, a key ROS, these antioxidants played an important part in detoxifying the cells and preventing damage linked to CI. This suggests that phenylalanine treatment enhances the fruit's antioxidant defense system, effectively minimizing oxidative stress and the associated CI symptoms in stored mangoes.[5] NO fumigation is a natural stress-mitigating agent that helped cold-stored 'Kensington Pride' mangoes combat the chilling stress.[56] NO plays an essential part in regulating ROS metabolism, which is crucial in minimizing oxidative stress caused by chilling temperatures. Exogenous NO downregulates the generation of ROS, such as H_2O_2, lowering the oxidative damage caused by CI. In addition to its antioxidant properties, NO was found to be involved in ROS signaling network, helping the mango's defense system respond more effectively to chilling-induced stress. By lowering ROS levels, NO safeguards cell membranes, maintains cellular homeostasis, and minimizes lipid peroxidation, which are key processes in protecting mango quality and reducing CI. Therefore, NO fumigation not only alleviates chilling stress but also enhances the mango's antioxidant capacity, delivering a protective mechanism against CI.[56]

Cold storage at temperatures below a commodity's chilling threshold temperature leads to chilling stress, which results in altered cellular functions due to the enhanced accumulation of toxic compounds, including ROS.[50] H_2O_2 acts as the primary stress response-signaling molecule. Polyols enhanced the enzymatic antioxidant system in cold-stored 'Palmer' mangoes by elevating

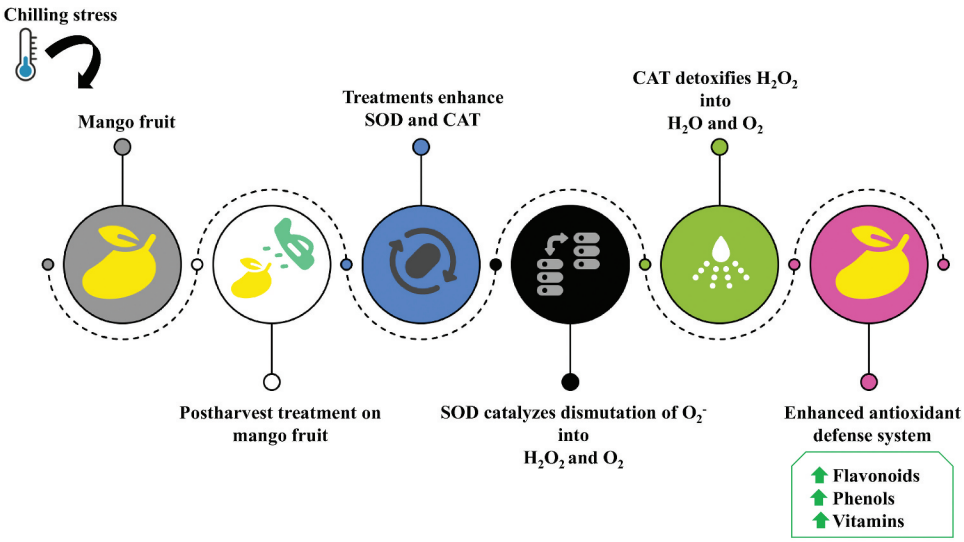

Figure 5. Chilling stress triggers oxidative damage in mango fruit. Postharvest treatments enhance SOD and CAT, boosting antioxidant defense. SOD converts O_2^- into H_2O_2 and O_2, while CAT detoxifies H_2O_2 into H_2O and O_2. This strengthens the antioxidant system by increasing flavonoids, phenols, and vitamins, improving mango quality under chilling conditions. CAT: Catalase, H_2O_2: hydrogen peroxide; O_2: Oxygen; O_2^-: superoxide anion; SOD: superoxide dismutase.

the SOD, CAT, and APX levels as well as the non-enzymatic antioxidant system comprising ascorbate-AsA. CAT catalyzes the H_2O_2 content produced and helps detoxify the fruit cell. APX utilizes AsA as an electron donor in order to eliminate H_2O_2. PPO results in quinone formation, which is responsible for the oxidation of phenolic compounds that are responsible for the pericarp browning of mangoes during CI.[18] Sorbitol-treated mangoes were found to down-regulate the PPO activity, which caused the mangoes to better retain membrane permeability. By decreasing the PPO activity, sorbitol successfully prevented the formation of quinones, thus inhibiting pericarp browning and maintaining the shelf-life of the produce.[18]

Treatment of 'Tainong' cold-stored mangos with 2,4-D enhanced the activities of CAT, SOD, GR, and APX.[74] In concert with ROS, LOX is a lipid oxidizing enzyme that converts cellular polyunsaturated fatty acids to lipid hydroperoxides, resulting in a loss of membrane integrity. 'Dashehari' mangoes treated with MT were reported to possess higher antioxidant properties due to enhanced activities of CAT, SOD, and APX than those used as control.[16] Spermidine coating on 'Langra' mangoes reduced fruit respiration, delayed chlorophyll discoloration, decreased metabolic activities, and enhanced AsA content.[75]

Promoting GABA shunt pathway

GABA is a non-proteinogenic, four-carbon compound amino acid that plays multiple roles in plants involving C-N metabolism, pH regulation, redox regulation, energy balance, and biotic and abiotic defense responses. The polycationic nature and low molecular weight of polyamines make them an essential component for plant growth and development. GABA biosynthesis is governed by two metabolic pathways including the GABA shunt and polyamine degradation. During stress conditions, the GABA shunt is supposed to be the main route for GABA accumulation. A study of MT-treated 'Langra', Chaunsa', 'Dashehari', and 'Gulab Jamun' mangoes revealed mainly GABA transaminase (GABA-T), succinic semi-aldehyde dehydrogenase (SSADH), and glutamic acid decarboxylase (GAD), to be the three enzymes involved in the GABA shunt pathway. GABA-T is believed to inhibit endogenous GABA accumulation, whereas, GAD contributes to the up-regulation of GABA-accumulating genes.[13]

Regulating arginine pathway and proline metabolism

Among the 20 amino acids responsible for protein formation, proline is an essential amino acid found in a free state and is synthesized from the ornithine or glutamate pathways. P5CS and ornithine-delta-aminotransferase (OAT) are the primary pathways for proline biosynthesis. Proline maintains cell homeostasis, detoxifies the ROS, and stabilizes the cell membrane integrity, thus protecting plants against oxidative stress. Proline accumulation has been reported to provide chilling tolerance to mangoes.[54] 'Keitt' mangoes, when treated with MT and stored for 21 d at 5 ± 0.5°C, 85–95% RH, experienced enhanced chilling tolerance due to enhanced proline accumulation and enhanced enzymatic activity of P5CS and OAT. Moreover, MT down-regulated the activity of PDH. PDH is a rate-limiting mitochondrial enzyme responsible for the degeneration of proline into glutamic acid; thus, lower PDH activity results in enhanced proline accumulation.[76] MT-treated cold-stored 'Langra' mangoes also experienced chilling tolerance due to endogenous proline accumulation.[77]

Up-regulating CBF genes

Transcriptional factors named C-repeat/dehydration-responsive element-binding factors (*CBF/DREBs*) mediate cold stress responses in plants.[78] They were first isolated from *Arabidopsis thaliana*.[79] *CBF*s are termed the first wave of cold-responsive genes.[80] The *CBF*s are responsible for transcribing multiple cold-regulated (*COR*) genes whose up-regulated expressions are required to combat chilling stress in plants.[81] A study of cold-stored 'Guifei' mangoes investigated the expression and relation of a full-length *CBF* gene (*MiCBF1*) with fruit chilling tolerance. LTC-treated cold-stored 'Guifei' mangoes experienced a several-fold up-regulation of *MiCBF1* genes compared to the control. *MiCBF1* genes were seen to follow a lower declining pattern when compared to the control and thus were known for cold acclimation in fruit.[59]

Although several strategies have been studied to mitigate CI in mango, their effectiveness greatly depends upon how they aim and coordinate key physiological pathways. While membrane stabilization is important in minimizing ion leakage and oxidative stress, research rarely examine how these mechanisms interact with energy homeostasis in CI-affected mango. Likewise, there are many studies on antioxidant system, there is limited report on how endogenous antioxidants can be upregulated via targeted metabolic interventions beyond exogenous treatments. The GABA shunt pathway, in spite of its acknowledged role in mitigate CI in mango, lacks comprehensive studies on how its activation corresponds with proline metabolism and arginine pathways. Interpreting these integrated pathways could help improve postharvest strategies, making them more target and effective rather than depending on generalized approaches.

Molecular approach involved in mitigating CI in mango

Mango fruit are highly vulnerable to low temperatures and prone to CI. Screening out the cold-resistance genes is highly needed to improve mango quality since CI severely limits the use of low temperature to extend mango postharvest life. Although CI is an area of extensive study, the molecular basis of CI events still needs to be explained and better understood. The novel transcriptomic technique helps us identify the metabolic changes (Fig. 6) and various genes affected and their structural changes. Treatment with SA, JA, and gibberellin (GA) have been reported to upregulate various genes in mangoes stored at 5°C that play vital roles during CI.[82] In mangoes stored at 5°C, within 2 d, the Mango *DELLA* (*comp13877*) gene is upregulated 4.5 folds.[41] Two isoforms of *NPR1 (comp20774, comp2117*) were also upregulated. JA treatment of mango has successfully mitigated CI by upregulating the gene *JAZ (comp20061, comp7092, comp6212)*. LTC-treated mangoes were identified to have upregulated *CBF* and *MiCBF1* gene. Using reverse transcription quantitative polymerase chain reaction (RT-qPCR), the expression of *MiCBF1* in response to LTC were examined. The analysis

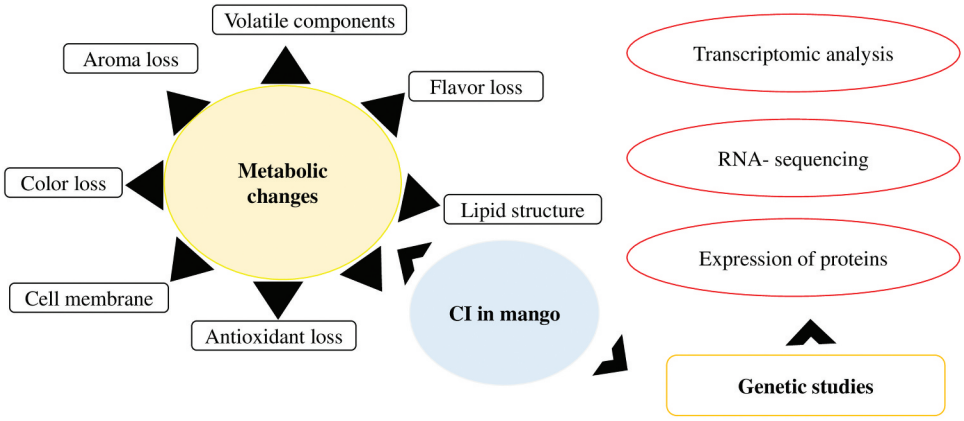

Figure 6. Schematic representation of the various areas studied to understand the chilling injury mechanism in mango.

revealed that LTC significantly upregulated the expression of *MiCBF1*, indicating its potential involvement in enhancing chilling tolerance.[59]

Proteomic analysis has highlighted the role of proteins involved in the antioxidant system, energy metabolism, hormone signal transduction, cell wall metabolism, secondary metabolism, and HSPs that play significant roles in CI of mango fruit. Further, proteins named GAPDH1, GAPDH2, SDH, ADK, and ACAA were found to be the determining factors that conclude the energy status of mango fruit under chilling stress.[58] Expression of HSPs in mango fruit peel during or after removal from cold storage results in CI reduction. Chilling stress leads to misfolding of proteins and causes them to accumulate in the endoplasmic reticulum (ER). Some protein processing transcripts, including the ER-associated degradation (ERAD) system, were seen to upregulate in the ER under chilling conditions, while SAR1 (comp21264, comp21135, comp21200) and Bip (comp24844) were the primary upregulated protein folding and transport genes. Transportation of the correctly folded proteins from the ER to the Golgi takes place through SAR1. Bip is an ER protein related to chilling stress.[45] Concerning the chilling temperatures, cold-stored mangoes showed upregulation of 36 ERAD genes. Thus, the processing of proteins in the ER plays a significant role in combating chilling stress.

Conclusions and future directions

Mango is a highly perishable fruit, and while cold storage is a common method for preserving its quality, extended storage at temperatures below its chilling threshold can cause CI. CI negatively impacts taste, flavor, appearance, and overall fruit quality, significantly reducing marketability and leading to postharvest losses. Addressing this issue demands a multifaceted approach integrating non-chemical, chemical, and molecular strategies. This review outlines the symptoms of CI in mango and discusses several strategies to combat it. Non-chemical treatments such as HWT, LTC, and CA storage, have demonstrated potential in alleviating CI symptoms by modulating cellular chilling-induced responses. Likewise, chemical treatments like SA, MT, NO, PROG, and CaLac, have shown efficacy in maintaining mango quality by stabilizing membranes, accelerating antioxidant activity, and modulating chilling stress-induced signaling pathways.

Despite these advancements, notable knowledge gaps remain. The specific molecular mechanisms underlying CI progression and tolerance are yet to be fully understood, demanding additional investigation. Advanced molecular approaches, including gene-editing (e.g., clustered regularly interspaced short palindromic repeats (CRISPR-Cas9), and ribonucleic acid interference (RNAi), hold promise for directly altering gene expression to improve mango cold tolerance. Also, the consolidation of omics-based studies, transcriptomics, proteomics, and metabolomics can impart deeper insights

into chilling stress-induced pathways, assisting in the development of more targeted interventions. Future research should also target real-time imaging techniques to trail CI development at the cellular level, as well as the capability of biodegradable coatings and nanotechnology-based formulation for limited release of protective compounds. Establishing a comprehensive understanding of CI at both physiological and molecular levels will be essential in developing sustainable and commercially viable solutions to maintain mango postharvest quality.

Author's contribution

H. Sati – Data curation, Formal analysis, Validation, Visualization, and Writing an original draft.
S. Pareek – Conceptualization, Supervision, Validation, Visualization, Reviewing, and Editing.
J. K. Brecht – Writing – reviewing and editing
E. M. Yahia – Writing – reviewing and editing

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No potential conflict of interest was reported by the author(s).

Data availability statement

No data was used for the research described in the article.

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