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Current Opinion in Biotechnology

Dissecting postharvest chilling injury through biotechnology

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Paradoxically, refrigerating many fruits and vegetables destroys their quality, and may even accelerate their spoilage. This phenomenon, known as postharvest chilling injury (PCI), affects produce from tropical and subtropical regions and leads to economic and postharvest loss and waste. Low temperatures are used to pause the physiological processes associated with senescence, but upon rewarming, these processes may resume at an accelerated rate. Chilling-injured produce may be discarded for not meeting consumer expectations or may prematurely deteriorate. In this review, we describe progress made in identifying the cellular and molecular processes underlying PCI, and point to advances in biotechnological approaches for ameliorating symptoms. Further, we identify the gaps in knowledge that must be bridged to develop effective solutions to PCI.

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Introduction

Refrigeration can lead to postharvest loss and waste (PLW), although it is the most effective strategy to maintain the quality and prolong the shelf-life of horticultural products. The rates of metabolic reactions increase 2–3-fold for every 10°C rise in temperature [1], and low-storage temperature delays deterioration by slowing down respiration and ethylene production, and by reducing pathogen growth and water loss. Commodities such as apples, blackberries, blueberries, cherries, and grapes benefit from refrigeration, however, in produce originating from tropical and subtropical regions, such as tomato, banana, pineapple, potato, and basil, refrigeration may lead to injury [2].

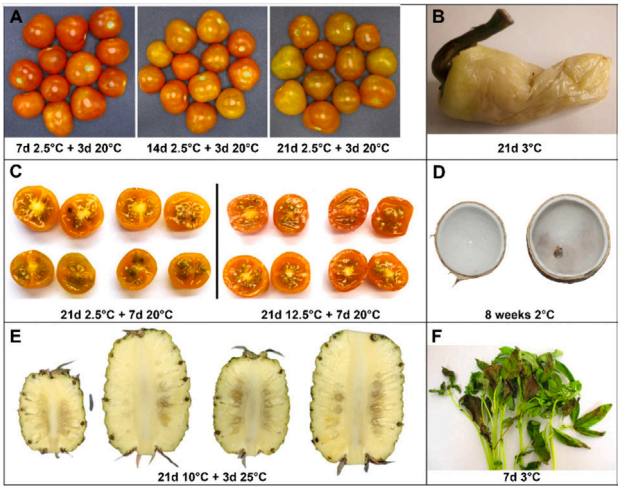
Postharvest chilling injury (PCI) is initiated when the tissues of cold-sensitive species are stored between 0 and 15°C, but becomes apparent after transfer to warmer conditions [2]. Because the affected species are taxonomically diverse and the organs affected vary, for example, fruit, tuber, root, leaf, and stem, PCI symptoms can be variable (Figure 1). However, some common phenotypes include tissue browning or blackening, pitted surfaces, shriveling, negative changes in texture, carbohydrates and aroma volatiles, and fungal infection [2,3••].

PCI severity is determined by many factors with temperature and storage time being the most important. If low temperatures are mild and exposure istransient, many metabolic functions will resume after rewarming, and visible symptoms may not develop. Under sustained low-temperature stress, tissue acclimation fails, leading to exhaustion and the onset of severe PCI [4] (Figure 1). Preharvest factors, including genotype, environmental variables, and agronomic practices, all interact to influence PCI severity [5]. PCI is more severe in tissues harvested before reaching horticultural maturity (which is common practice), as the developmental pathways are incomplete and will be largely disrupted by chilling and rewarming [6].

Economic losses due to postharvest chilling injury

Although PCI is a significant problem, determining the PLW that can be ascribed to PCI is challenging because of the difficulty in identifying when it occurs. Most damage appears in retail outlets or in consumers' homes, which is hard to monitor. Further, symptoms are internal in many species, for example, pineapple, nectarines, and so on, and some abnormalities in texture and flavor are only detected when the fruit or vegetable is eaten [2,7••] (Figure 1). PCI symptoms are also misdiagnosed. For example, PCI increases susceptibility to pathogens, which is often mistaken as the primary cause of loss, and poor-quality produce due to PCI may be attributed to early harvest or poor varietal selection [8].

Figure 1



PCI symptoms in horticultural products. **A**. Progressive loss of surface color proportional to increasing storage time at 2.5°C in tomato fruit cv. 'Micro-Tom'. **B**. Tissue maceration and pedicel discoloration in chili pepper. **C**. Seed browning in rewarmed tomato fruits cv. 'Sungold' after 2.5°C storage compared to a control non-chilling temperature (12.5°C). **D**. Internal browning (IB) in coconut cv. 'Nam Hom'. **E.** IB in pineapple cv. 'Pattavia'. **F.** Leaf browning and necrosis in basil. Photo credits: Karin Albornoz and Kietsuda Luengwilai.

Given the above factors, quantifying economic losses due to PCI is also difficult. The global trade of fresh fruits and vegetables was worth 115 billion USD in 2018 [9]. More than half of the 50 highest-traded global commodities are PCI-susceptible [10], and PLW globally is estimated at ~33%. If PCI reaches even 0.5% of PLW, it could cost USD $144 M. Additional costs related to 1) shipping at temperatures higher than the commonly used 4°C, and 2) the complex logistics that factor in harvest date and storage life into transportation, are not included into this estimate, but they collectively reduce flexibility for growers and distributors.

Periodically, the apparent benefits of extending shelf-life by storing produce at inappropriate temperatures may outweigh the negative impact on quality: if fruit are stored at non-PCI-inducing temperatures for the equivalent time, they may spoil and will be rejected, whereas fruit with invisible PCI symptoms are salable. This incentivizes refrigerating sensitive produce, which may be profitable in the short term, but leads to long-term consumer distrust in produce quality and value [11,12].

Biological processes underlying postharvest chilling injury molecular pathways

The abnormalities associated with PCI that lead to consumer dissatisfaction, waste, and loss can be linked to specific cellular dysfunctions (Figure 2). Mealy texture, surface pitting, and fungal susceptibility are due to reduced pectin solubilization and depolymerization [13], and microfractures in the cell-wall network [6].

Tissue browning is initiated when organelles lose their structural integrity in chilled tissues. Chilling leads to membrane disassociation that releases polyphenol oxidase, peroxidase, and their phenolic substrates into the cytosol where they react to form quinones [14]. Polymerization of quinone creates the brown pigments in chilling-injured tissues [15].

The physiological diversity of fresh fruits and vegetables will lead to differences in the molecular processes affected by PCI, which can be summarized as follows:

Fruit

Cold storage disrupts the finely-tuned ripening program that is modulated by the interplay of hormones, transcriptional factors (TFs), and epigenetic marks [16] often, with negative consequences for fruit quality [17,18]. Upon rewarming, increases in respiration and ethylene production are initiated, and visible chilling-injury symptoms develop, the magnitude of which is inversely proportional to the storage temperature [19••]. Even mild chilling injury in red tomato fruit triggers epigenetic changes in ripening TFs such as RIN, NOR, and CNR that downregulate the production of key volatiles responsible for hedonistic values [3••]. However, this is not always so, 'abnormal chilling injury behavior' occurs at milder storage temperatures and has been reported in peach and nectarine [20], plum [21], persimmon [22], and papaya [23,24]. The mechanisms underlying 'abnormal chilling injury' are unknown, but the enhancement of sugar and energy metabolism may be relevant.

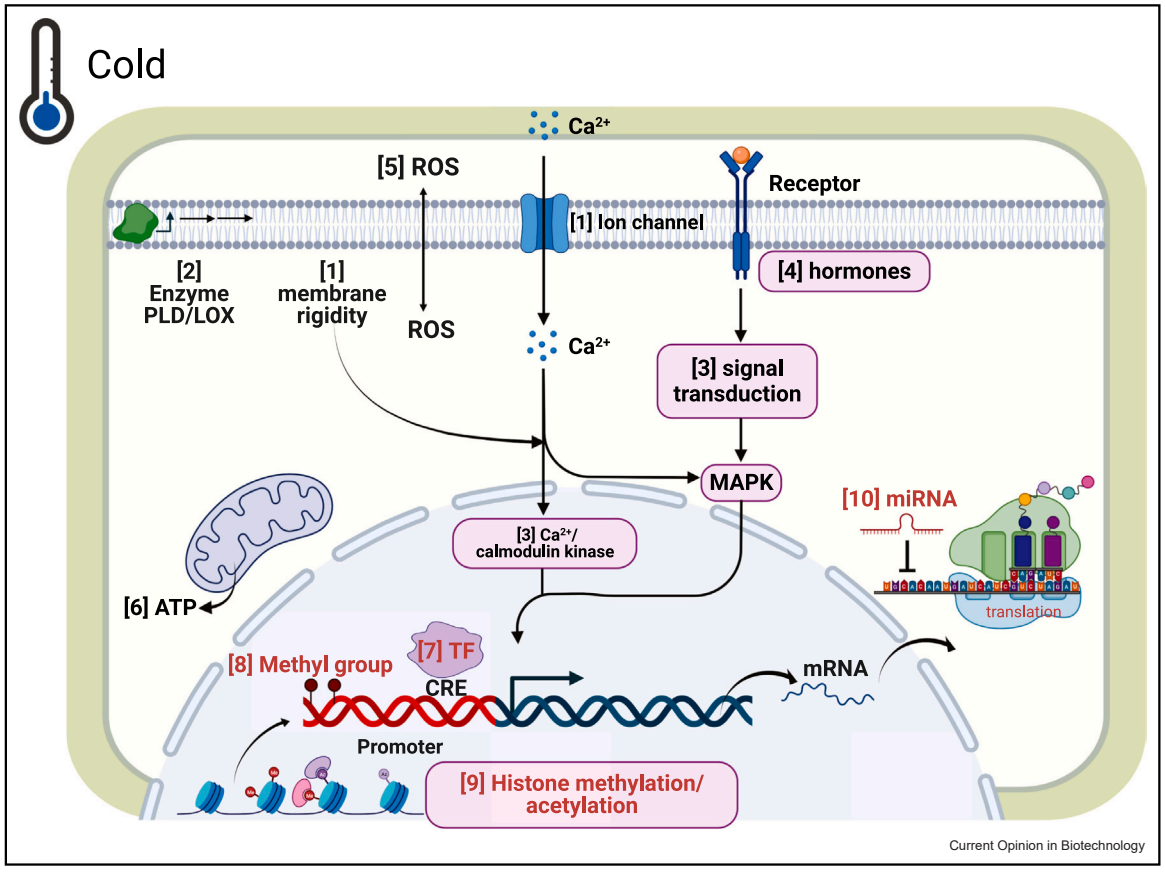
Produce harvested at immaturity

Many economically important commodities, for example, zucchini, cucumber, and bell pepper, are harvested before reaching physiological maturity, and will thus have different cold-stress responses to those commonly studied such as tomato and banana, which are harvested when mature [25]. Commodities harvested at immaturity typically have higher respiratory and deterioration rates, greater water loss because of incomplete cuticle development, and inefficient reactive oxygen species (ROS) scavenging systems [25], which will influence their PCI response.

Storage tubers

In potato, chilling leads to cold-induced sweetening (CIS) — starch breakdown and sugar accumulation (Figure 3) [26], where the latter serves as protective compatible solutes [27]. When these 'sugared' tubers are fried, baked, or roasted, they turn black as acrylamide

Figure 2



A composite diagram showing elements of the cellular and molecular response to cold stress. Although many tissues experience PCI, most of the data are derived from tomato and may not be universal. **(1)** Chilling stress alters membrane composition and fluidity [77,78], cytoskeleton rearrangement, and calcium-channel functioning, leading to uncontrolled ion influx into the cytoplasm [79]. **(2)** Changes of cell-membrane composition and fluidity are caused by phospholipid hydrolysis enhanced by PLD and LOX activities [80,81], and by altering membrane-bound enzyme activity [82,83]. **(3)** Second messengers and a series of phosphorylation and dephosphorylation reactions amplify the cold signal [79,84]. Ca^{2+} is one of second messengers. Cold-induced changes in cell membrane, affect the transmembrane receptors responsible for Ca^{2+} regulation. Activation of Ca^{2+} induces mitogen-activated protein kinases (MAPK) and Ca^{2+}/calmodulin (CaM)-dependent kinases for downstream transcriptional regulation [85]. In other species, *C*-repeat binding factor (CBF)-independent pathways may regulate the upstream chilling-induced hormonal signal-transduction response [86]. **(4)** Plant hormones, including ethylene, abscisic acid, auxin, jasmonic acid, gibberellins, and brassinosteroids, have been shown to influence MAPK cascades, which are important for propagating the cold signaling through the CBF-mediated pathways [87]. **(5)** Cold causes oxidative stress, and reactive oxygen species (ROS) accumulate to harmful levels due to inefficient scavenging, causing oxidative damage, and further membrane peroxidation [88,89]. **(6)** Decreased levels of ATP, and increased rates of respiration and ethylene production, reflect global metabolic disruption and imbalanced energy status [90–92]. The sections labeled in red are related to transcriptional and translational regulation: **(7) C**old-responsive TFs differentially bind to the *cis*-regulatory elements (CREs) of cold-responsive genes to modulate their expression. **(8)** Gene expression is also regulated by the DNA methylation status of the promoters of some cold-responsive genes [3••]. Further, **(9)** the methylation and acetylation status of histones regulate tomato fruit ripening. Histone demethylases SlJMJ6 [93] and SlJMJ7 [94], and histone deacetylase SlHDT1, are key regulators of ripening [95], but their cold responsiveness has not been yet determined. **(10)** Micro-RNAs (miRNAs) can regulate gene expression post-transcriptionally. Sly-miR164a is a negative regulator of some aspects of PCI, by changing hydrogen peroxide levels and fruit firmness [96].

forms, which is visually unappealing, bitter in taste, and harmful to human health [28].

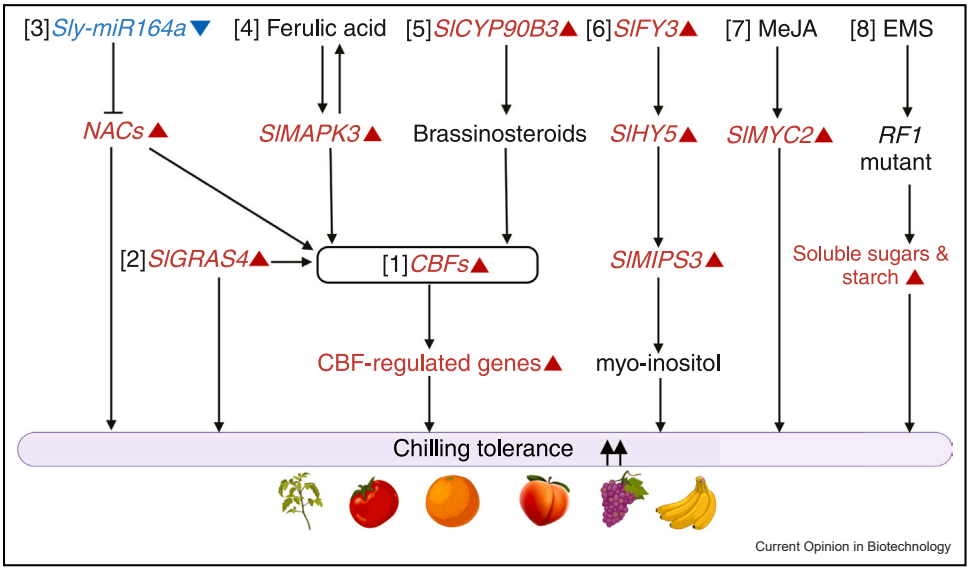
Leafy greens

The shelf-life of leafy greens is relatively short, given their limited energy reserves and high transpiration rate. Fresh basil is a popular herb with high export value, but chilling causes changes in leaf photosynthetic parameters and stimulates ethylene biosynthesis, which accelerates senescence [29,30] (Figure 1F). Loss of membrane permeability, suppression of the protective antioxidant system, tissue browning, and *Botrytis* attack, all lead to premature spoilage [29].

Gene targets for postharvest chilling injury improvement

Reducing the severity of the negative traits of PCI that lead to waste and loss could be achieved by inducing

Figure 3



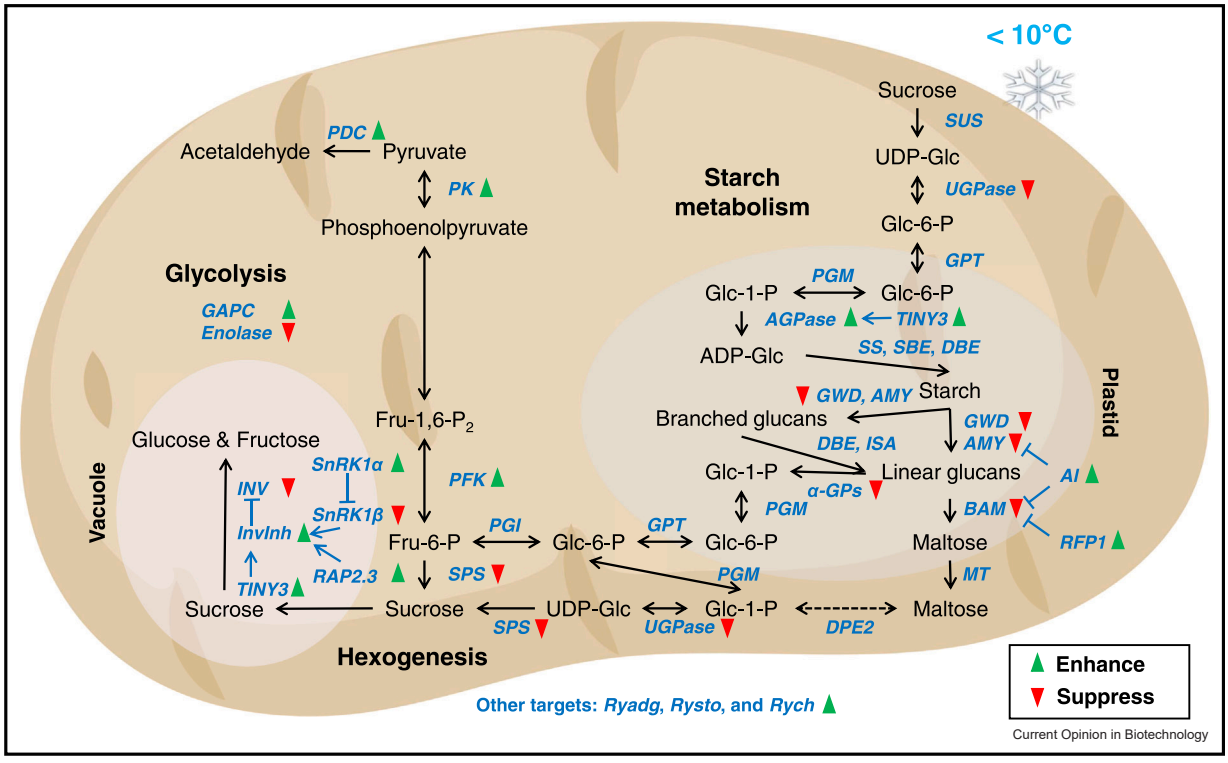
A summary of changes in the expression of genes that are associated with alleviating chilling injury. When the gene in blue was suppressed, or the genes in red were increased, tissues had reduced PCI symptoms. The blue and red triangles indicate that the gene is negatively or positively correlated with chilling tolerance, respectively (please note — the physical position of elements in the diagram does not reflect their importance). **(1)** The CBF transcription-factor family is at the center of this diagram, because of the importance of this signaling pathway in cold response (reviewed in Hwarari et al., 2022) [97], but there are also CBF-independent cold-tolerance pathways. Recent examples include *CBF1* in citrus [98], *CBF6* in peach fruit [99], and *CBF4* in grapevine plants [100], while knocking out *SlCBF1* in tomato seedlings led to severe CI symptoms [101]. **(2)** Overexpression of *SlGRAS4* improved chilling tolerance by CBF-independent and -dependent pathways [32•]. **(3)** *Sly-miR164a* was knocked down by tandem target-mimic structure, alleviating chilling injury and enhancing the *NAC* gene expression and ABA contents in tomato fruit [96]. **(4)** Exogenous ferulic acid enhanced chilling tolerance by inducing *SlMAPK3* and *CBF* expression, knocking out *SlMAPK3* by CRISPR/Cas9 decreased PCI tolerance in tomato fruit [102]. **(5)** Overexpression of *SlCYP90B3* decreased PCI by increasing brassinosteroid content and upregulation of *CBF* genes [33•]. **(6)** SlFY3 physically binds to SlHY5, enhancing *SlMIPS3* expression by binding to its promoter. *SlMIPS3* is important in myo-inositol synthesis, and increased myo-inositol-alleviated chilling-injury symptoms. Overexpression of *SlFY3* or *SlHY5* individually alleviated chilling symptoms, and silencing *SlFY3*, *SlHY5*, or *SlMIPS3* enhanced chilling susceptibility in tomato plants [103–105].**(7)** MeJA application increased *SlMYC2* expression, a TF involved in MeJA signaling, and chilling tolerance was increased. Silencing *SlMYC2*, resulted in fruit with high PCI [106,107]. **(8)** An ethyl methanesulfonate (EMS) mutant in banana called *RF1* had enhanced chilling tolerance, potentially by increasing carbohydrates [108].

allelic diversity at single or multiple genes that directly regulate relevant pathways (Figure 2). Integration of multi-omics data of cold-injured tissue compared with non-chilled tissues, has helped identify gene targets that influence PCI [3••,31] (Figure 3).

In tomato, two important discoveries were made from genes identified using functional genomics: over-expressing the TF *SlGRAS4* reduced fruit-surface pitting, and promoted a more uniform color due to increased β-carotene content after chilling [32•]. Likewise, over-expression of *SlCYP90B3*, a key brassinosteroid biosynthetic gene, improved the antioxidant response of fruits during cold storage, reducing PCI [33•]. These genes coordinated multiple pathways to improve PCI tolerance (Figure 3).

Candidate genes for improving PCI tolerance have also been found by applying physical and chemical treatments that alleviate symptoms, and by studying the associated changes in the signal-transduction pathway. This is an active area of research where the literature is expanding rapidly [34]. For example, physical treatments such as dipping in hot water before chilling mitigated fruit PCI, and have been associated with the upregulation of heat-shock proteins in banana [35] and in mango [36,37], among others. The *MaAPY* gene family and the ATP receptor MaDORN1.19 are likely to be important for maintaining ATP homeostasis under chilling, after exogenous application of ATP or GTP to banana fruit [38,39]. TFs *MabHLH060* and *MabHLH183*, which are associated with reduced cold-induced membrane rigidity, were induced by Ethrel®, an ethylene-releasing agent, which also reduced banana fruit PCI visual symptoms [40]. Melatonin reduced peel browning in bananas, by inducing miR528 expression, which in turn downregulated several 'browning genes', i.e., *MaPPO1*, *MaPPO2*, and *MaPPO3* [41]. In tomato fruit, melatonin improved surface pitting, increased the expression of *FAD3* and *7*, and reduced the expression of

Figure 4



Gene targets in potato tuber that alter chilling-induced sweetening. Carbohydrate metabolic pathways associated with CIS in tuber were modified from Zhang *et al*., 2017 [49]. Green arrows indicate when enhancement of gene expression would alleviate the CIS phenotype and red arrows show when suppression of that gene reduced CIS symptoms. **Key**: Genes are shown in blue: *SUS*, sucrose synthase; *UGPase*, UDP-glucose pyrophosphorylase; *GPT*, glucose-6-phosphate/phosphate translocator protein; *PGM*, phosphoglucomutase; *AGPase*, ADP-glucose pyrophosphorylase; *SS*, starch synthase; SBE, starch-branching enzyme; *DBE*, debranching enzyme; *AMY*, alpha-amylase; *ISA*, isoamylase; *α-GPs*, α-glucan phosphorylase; *DPE2*, disproportionating enzyme; *MT*, maltose transporter protein; *AI*, amylase inhibitor; *RFP1*, ring finger protein 1; *PGI*, glucose-6-phosphate isomerase; *InvInh*, invertase inhibitor; *RAP23*, ERF-VII transcription factor; *SnRK*, SNF-related serine/threonine-protein kinase; *TINY3*, a CBF/DREB transcription factor; *GAPC*, cytosolic glyceraldehyde-3-phosphate dehydrogenase; *PFK*, phosphofructokinase; *PK*, pyruvate kinase; *PDC*, pyruvate decarboxylase; *Ryadg*, *Rysto*, and *Rych*, a locus containing three genes. **Metabolites**: UDP-Glc, UDP-glucose; Glc1P, glucose-1-phosphate; Glc-6-P, glucose-6-phosphate; Fru-6-P, fructose-6-phosphate; ADP-Glc, ADP-glucose; Fru-1,6-P2, fructose-1,6-bisphosphate.

phospholipase D (*PLD*) and *lipoxygenase* (*LOX*) genes, which helped to maintain membrane integrity under cold stress [42].

New insights into regulatory networks governing PCI can be gained through-omics profiling as shown in several examples. Treating peach fruit with methyl-jasmonate (MeJA) delayed internal browning (IB), maintained fruit texture and aroma volatiles, and the accompanying transcriptomic and methylomic changes were revealed [43]. In bell pepper, MeJA reduced surface pitting, shriveling, discoloration, and seed browning, and differences in the transcriptome, proteome and metabolome compared with untreated fruit were detected [44]. Other studies combined cold storage with additional factors such as varying carbon dioxide, or fruit harvested at different times, and identified differentially expressed transcripts by RNASeq [45,46]. These differential transcripts, proteins, and metabolites may help to identify gene networks and their regulators for genetic engineering.

Gene targets for minimizing CIS in potato have been identified. CIS has been extensively studied compared with PCI in fruit, because potato is a staple for one billion people [47], and in some production areas, tubers are stored at low temperature for up to eight months [48]. During tuber storage, there are cycles of synthesis and degradation of both sucrose and starch, but at temperatures between 4 and 10°C, the degradative fluxes are activated, so that reducing sugars accumulate (Figure 4). This change in metabolism occurs via the upregulation of genes encoding the beta-amylase, glucan water dikinase, sucrose phosphate synthase, and invertase enzymes [49] (see Figure 4 for details). Attempts to alleviate CIS by modulating the activity of core enzymes of carbohydrate metabolic pathways have been made, although the role of each enzyme isoform is still to be elucidated. Recently

identified non-metabolic genes that regulate CIS (Figure 4), for example, A CBF/DREB transcription factor (*StTINY3)* [50•] and *ring finger protein 1* (*RFP1*) [51], are good targets for developing new germplasm.

Longer-term biotechnological solutions

There is an acute need for a greater foundational understanding of PCI. Several advances have been made in model species, where regulatory elements of the cold signal-transduction pathway response have been identified and functionally verified. Integrating the discrete 'snapshot' studies discussed previously into full models across tissues, developmental stages, and conditions, is the next step for developing functional biotechnological solutions.

Spatiotemporal regulation

PCI is often assessed in a single tissue sampled from a defined region. Not only is valuable information about the spatial evolution of the process lost [52,53], but events occurring in all the tissues that are consumed are not captured. A few studies have addressed this gap and serve as a guideline for future work. In tomato, tissue-specific development of PCI was detected, even though pericarp is usually the only tissue traditionally studied [19••]. In pineapple, scanning electron microscopy and histochemical staining of fruit revealed that IB starts at the phloem and diffuses throughout fruit tissues from the core [54]. A breakthrough was made when a high-resolution spatiotemporal transcriptome atlas in tomato was developed, which showed that ripening is not homogeneous [55••]. Because cold interferes with fruit ripening, some PCI symptoms would be expected to occur heterogeneously. Looking holistically at the chilling response across cells and tissues in harvested organs would uncover additional regulatory features of PCI.

Fine-tuning gene expression

Uncontrolled and physiologically abnormal expression of genes through genetic engineering may severely disrupt the multiple finely-balanced gene-regulatory networks, resulting in deleterious phenotypes, especially if constitutively expressed in tissues where they do not normally occur [56]. Regulated promoter systems to direct tissue gene expression in a highly controllable manner, with spatial and temporal precision [57], may be useful to study and design long-term solutions to PCI. Sequential changes in gene expression by promoter engineering are also a promising approach [58–60]. Precise editing of chilling-associated *cis*-regulatory elements (CRE) and differentially methylated regions due to chilling by Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR) could promote ripening under chilling conditions and alleviate PCI (see Figure 5 for detailed explanation). Achieving this precision is an immensely challenging prospect that likely depends on attaining the previously described holistic knowledge of chilling response.

Challenges to studying and ameliorating postharvest chilling injury

There are many longstanding challenges related to PCI that remain largely to be tackled, and which limit progress. The nature of research appears fragmented, and many species are studied with a substantial focus on symptom alleviation through exogenous treatments rather than development of endogenous/innate solutions. The importance of PCI is reflected in the number of papers published in Google Scholar using the search term '*Postharvest chilling injury*', which has increased 7-fold over the past 20 years (2001–2021). This directly points to the urgency of developing biotechnological approaches to address PCI, and the immediacy with which solutions are needed.

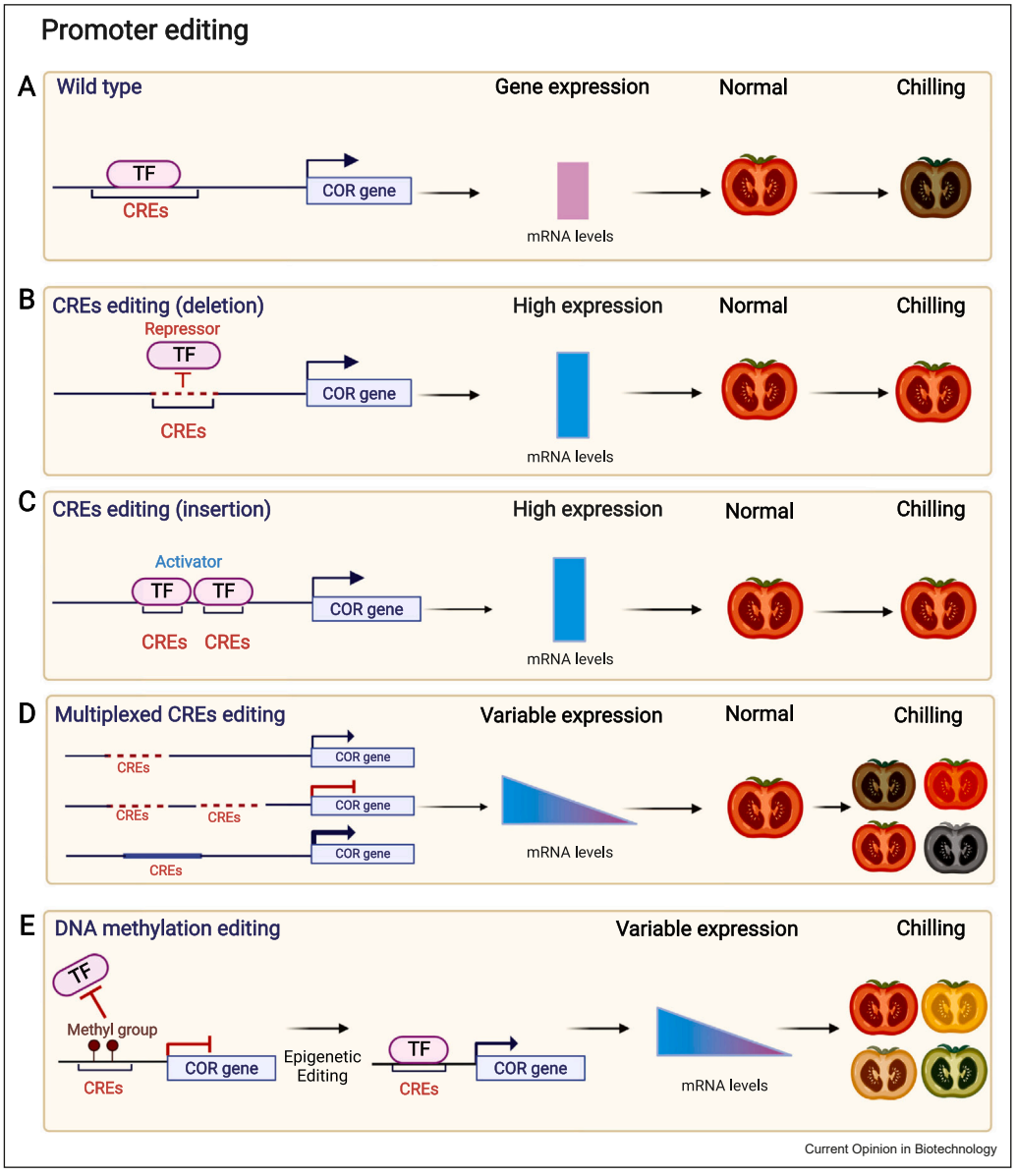
Variability of the postharvest chilling injury response

Environmental and management factors, both pre- and postharvest, influence whether a tissue will manifest PCI after cold storage. Time of year, time of day of harvest, and the growing environment (i.e., climatic events, daylength, humidity, soil, and day and night temperature) are all documented to influence the trait [61,62]. Experiments are by necessity, multifactorial, and rely on large harvests of fruit, tubers, and so on, which limit the number of experiments that can be set up. In addition, plants must reach advanced developmental stages to obtain fruit or tubers, and this is followed by weeks of postharvest cold storage, limiting the number of experiments that can be performed in a year. This is exacerbated in perennial crops that fruit annually and may be biennial, offering fewer opportunities for experimentation. Replication of experiments may not be economically feasible, therefore, at a minimum, a thorough reporting of these factors should be included in PCI studies [4,63].

Knowledge of cold signal-transduction pathways is based on actively growing plants

Light and carbon availability follows a diurnal cycle creating different signaling inputs [64–66]. There is a limit to which the data so derived can be translated to PCI [64]. The growing plant may use avoidance, escape, and tolerance to cope with cold [67], while in contrast, options for surviving anthropogenic cold stress in stored tissues with limited nutrients are few [19••,68]. Cold-responsive genes in *Arabidopsis* rosettes may have conserved functions in leafy greens, but genes and pathways from model crops, for example, cereals, will have limited relevance to the consumed tissues in horticultural crops [69]. Therefore, postharvest studies must redescribe the behavior of these pathways under the conditions of each experiment, which is laborious and expensive or work with tempered assumptions about them.

Figure 5



. **Strategies for engineering PCI phenotypes by disrupting promoter *cis*-regulatory elements (CREs) or their DNA methylation fingerprint in candidate cold responsive (COR) genes.** CREs are DNA sequences often found in gene promoters that are bound by specific TFs upon developmental or environmental triggers. **(A)** TFs can accelerate or slow down the production of mRNAs of the gene by binding the CREs under normal condition, bind the CREs of multiple genes in a related pathway, or bind the CREs of itself or other TFs. Examples show how CRE mutations may increase the expression of genes that lead to cold tolerance. **(B)**CRE deletions can prevent binding of a repressor TF. **(C)** If the TF is an activator, engineering additional copies of the cognate CREs would amplify gene expression. **(D)** Multiplexed editing of chilling-associated CREs with multiple gRNAs could potentially generate lines with a range of phenotypes as seen in developmental traits [59]. **(E)** Chemical modifications of DNA such as direct methylation of the CREs, or methylation or acetylation of neighboring histones that result in the physical remodeling of chromatin, would influence TF access to CREs and transcription. Key in (**D**) the red dashed lines indicate deletions; arrow thickness indicates relative expression strength, andthe blue line indicates a sequence insertion.

The events that initiate postharvest chilling injury are poorly understood

The question of if there is a single primary event that triggers others, or if multiple events occur simultaneously, remains. ROS production, and membrane disassembly are cited as incipient processes, but their relative timing has not been resolved, as there are contrasting reports of their relative importance [6,70]. Studying biological process hours after chilling would illuminate the rapid and early, cold-tolerant responses

that are often overlooked. Understanding the progression of these events in different tissues could allow for more targeted and efficient solutions in alignment with the spatial and temporal occurrence of PCI events.

Research is focused on a few model species

Molecular components of the chilling pathways in tomato, peach, banana, and potato have been identified because of their economic importance and advanced functional genomics tools, while research on other species lag. However, whole genome sequencing of diverse crops such as pineapple, coconut, and basil [54,71,72] is fueling PCI research in these species. Bridging the technological gap for PCI research in tropical species would benefit multiple stakeholders, astropical commodities are rich in bioactive compounds and have exotic tastes and flavors [73], of interest to international markets. These crops are likely to suffer from PCI that increases export costs, since air transport, rather than maritime shipping, would be needed.

Applying synthetic biology principles

Reliable and efficient transformation systems would accelerate a systematic approach to engineering PCI [10,74]. Candidate genes would be designed by editing their sequence, and the performance of the 'built' or engineered crops under chilling, tested and observed [75]. Through an iterative and systematic 'Design–Build–Test–Learn' process, we may identify novel genes that influence PCI, developing resistant varieties contemporaneously with basic discovery.

Integrating research into the postharvest value chain

New varieties with improved PCI traits must be reproducible under commercial conditions to be successful. Most PCI research is done under lab conditions, and this disparity must be reconciled to ensure consumer satisfaction [76]. Research that spans the lab-to-table continuum is therefore critical.

Conclusions and perspectives

Crops bred with increased resiliency to PCI would save financial and environmental resources, improve consumer satisfaction, and encourage higher consumption of produce with better public health outcomes. Poor awareness of PCI and difficulties in its identification make determining the economic value of losses associated with this disorder challenging, making it hard to justify greater investment in a broader range of species. The result is that the resources needed to systematically tackle PCI are not available. Still, as shown here, recent advances in plant functional genomics are increasingly being leveraged to discover the genes and mechanisms that regulate postharvest chilling for biotechnological improvements.

CRediT authorship contribution statement

Karin Albornoz: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **Jiaqi Zhou:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **Jingwei Yu:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **Diane M Beckles:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision.

Data availability

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

Conflict of interest statement

The authors declare that there is no conflict of interests.

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- • of special interest
- •• of outstanding interest.

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