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RECEIVED 06 September 2025

ACCEPTED 02 October 2025

PUBLISHED 15 October 2025

CITATION

Niu J, Bao H, Jiao S, Han H
and Wang G (2025) Harnessing peptide
hormones for postharvest preservation
of horticultural produce.
Front. Plant Sci. 16:1700360.
doi: 10.3389/fpls.2025.1700360

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Harnessing peptide hormones for postharvest preservation of horticultural produce

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KEYWORDS

horticultural produce, peptide hormone, postharvest preservation, shelf life,
small peptide

Introduction

Horticultural postharvest losses, including reductions in quantity, quality and appearance from harvest to consumption, pose a significant global challenge to the supply chain and economic sustainability. Postharvest losses occur more frequently in fruits and vegetables due to their high moisture content, bulkiness, and high respiratory rate as living tissues (Ali et al., 2025). Furthermore, the seasonality, regionality, and perishability of fresh fruits and vegetables substantially complicate postharvest storage and shelf life, ultimately affecting consumer acceptance. Accumulating studies focused on addressing postharvest losses in horticultural produce, underscoring the importance and essential role of innovative preservation technologies to mitigate this challenge. To date, a plethora of methods including physical preservation (e.g., cold storage, modified atmosphere storage, edible coatings, heat treatment, and irradiation), chemical preservation (e.g., 1-methylcyclopropene (1-MCP), calcium chloride, hydrogen sulfide, diphenylamine, and synthetic compounds), and biological preservation (e.g., antibiotics and bacterial inhibitors) have been shown to effectively prolong the supply period and maintain the nutritional quality of fruits and vegetables (Sridhar et al., 2021; You et al., 2022; Gomes et al., 2023). However, conventional preservation methods present significant environmental and safety concerns. Physical refrigeration, for instance, carries a high environmental cost due to its substantial energy consumption and carbon emissions. Chemical preservatives such as diphenylamine not only pose environmental pollution risks but also cause adverse health effects including skin hypersensitivity, tissue dysfunction, impaired endocrine function, and cancer (Ahmed et al., 2022). While effective, 1-MCP can impair fruit quality like flavor, aroma, and color, and may even induce abnormal texture or trigger physiological diseases in

certain horticultural products (Ahmed et al., 2022). Furthermore, current biological preservation methods are often hampered by unstable efficacy, high development cost, and complex application technologies. Consequently, the development of more efficient, stable, cost-effective, and environment-friendly strategies are imperative to mitigate potential these adverse impacts on human health and the environment.

Small peptides are short-chain biological molecules, typically consisting of 2–100 amino acids, that are generally classified into conventional peptides and non-conventional peptides (Krouk et al., 2023; Ji et al., 2025; Zhang et al., 2025). Conventional peptides are derived from well-characterized coding regions or standard open reading frames (ORFs), consisting of post-translationally modified peptides, cysteine-rich peptides, and non-cysteine-rich/non-post-translationally modified peptides (Ji et al., 2025; Zhang et al., 2025). Peptide hormones predominantly comprise post-translationally modified peptides and cysteine-rich peptides. In contrast, non-conventional peptides, such as micropeptides and small ORF-encoded polypeptides, originate from noncoding regions, including untranslated sequences, introns, non-coding RNAs (pri-miRNAs, long non-coding RNAs, and circular RNAs), intergenic regions, and other non-coding sequences (Zhang et al., 2025). As critical regulators with multifaceted roles, small peptides function in diverse fields such as medicine, cosmetics, food preservation, animal nutrition and healthcare, and plant growth and defense (Fan et al., 2022; Krouk et al., 2023; Zhang et al., 2023; Ji et al., 2025; Zhang et al., 2025). Their versatile functionality is attributable to a combination of favorable properties, including abundant sources, structure diversity, high specificity, membrane permeability, biodegradability, low toxicity, and complex receptor interactions (Fan et al., 2022; Zhang et al., 2023, 2025).

Currently, small peptides used in fruit ripening and postharvest management predominantly are non-conventional peptides, including antimicrobial peptides, antioxidative peptides, and peptides that providing physical barrier and/or regulating protein-protein interactions (Fan et al., 2022; Zhang et al., 2023). For instance, NOP-1, a small non-conventional peptide derived from the C-terminal part of the Arabidopsis ethylene regulator ETHYLENE INSENSITIVE2 (EIN2), binds to the ETHYLENE RESPONSE1 (ETR1) receptor. The binding prevents the formation of the EIN2-ETR1 protein complex in tomato, thereby blocking ethylene signaling and delaying the ripening process when applied to tomato (*Solanum pimpinellifolium* L.) fruit surface; furthermore, a significant delay in maturation and reddening is observed for exogenous applications of NOP-1 via injection, incubation, or surface application (Bisson et al., 2016; Milić et al., 2018). However, unlike conventional peptides, the non-conventional peptides are derived from highly divergent biosynthesis and processing routes which heavily hinders their identification, functional studies, and exploration of their molecular mode-of-action. In this regard, the classic type of conventional peptides, especially the peptide hormones with clear functions and well-defined molecular mechanisms, represent potential candidates to develop novel preservatives for extending storage and shelf life of horticultural products.

Peptide hormones are critical regulators in plant plasticity under abiotic and biotic stress

Plant peptide hormones are the classic type of conventional peptides which mediate cell-to-cell communications across diverse biological processes (Ji et al., 2025; Zhang et al., 2025). Typically, mature peptide hormones are undergone proteolytic processing and post-translational modifications from prepropeptides, which commonly harbor an N-terminal signal peptide for secretion, a variable intermediate sequence, and a conserved functional domain (Zhang et al., 2025). Subsequently, matured peptide hormones are secreted into the apoplast, where they diffuse to target cells over several cell layers or travel a long distance via xylem and phloem (Zhang et al., 2025). Commonly, peptide hormones are perceived by the membrane-localized receptor(s) to (de)activate either long-distance or local signaling pathways, thereby orchestrating plant developmental plasticity and stress resilience via (post) transcriptional, (post)translational, and/or epigenetic regulations (Ji et al., 2025; Zhang et al., 2025). Extensive studies have shown that peptide hormones are comprehensively implicated in, but not limited to, diverse biological processes such like stem cell homeostasis, organogenesis, fertilization, senescence, abiotic stress responses, and plant-pathogen interactions (Ji et al., 2025; Zhang et al., 2025). Particularly, peptide hormones are deeply implicated in the signaling and/or biosynthesis of phytohormones such as ethylene (Wang et al., 2016; Zhang et al., 2025), which is the gaseous ripening hormone notably influencing the postharvest physiology of the fruit. Importantly, many peptide hormones are able to confer tolerance to senescence, cold stress, and pathogen diseases which are deleterious during postharvest storage. Although significant advances have been achieved in understanding peptide hormones, the translation of this knowledge into practical applications remains limited. In this regard, peptide hormones with defined roles in crosstalking with ethylene or conferring tolerance to senescence, cold stress, and pathogen diseases are promising candidates for postharvest longevity.

Peptide hormones in preservation of postharvest horticultural products

Growing evidence have now surfaced that small signaling peptides can be used to delay fruit ripening and senescence and deterioration of horticultural produce, thereby reducing postharvest losses and maintaining commercial value (Figure 1; Table 1). The CTG134 peptide, a ROOT GROWTH FACTOR/GOLVEN (RGF/GLV) peptide that is transcriptionally activated by 1-MCP, is essential for maintaining the balance between auxin and ethylene during peach (*Prunus persica* L. Batsch) ripening and thus extending peach fruit storage duration (Tadiello et al., 2016). It was further shown that there are significant differences in peptidome between melting-flesh (“Zhongyoutao No.13”) and stony-hard peach (“Zhongyoutao No.16”) cultivars during

ripening. Those differentially abundant peptides are found to be predominantly involved in starch and sucrose metabolism, glycolysis, and ribosome synthesis, suggesting that these metabolic pathways are involved in peach fruit ripening and providing a theoretical reference for further exploring of RGF/GLV peptides in regulating peach fruit ripening and senescence (Li et al., 2022). Exogenous application of another peptide hormone, PHYTOSULFOKINE (PSK), can effectively retard yellowing and preserve the nutritional integrity of broccoli (*Brassica oleracea* L.var. *italica* Plenck) florets under cold storage through elevated levels of guanosine 3', 5'-cyclic monophosphate (cGMP), phenols, flavonoids, and ascorbic acid (Aghdama et al., 2020). In addition, exogenous PSK application has been also shown to delay yellowing in broccoli florets by increased activities of methionine sulfoxide reductase, antioxidants, cysteine peroxidase, and enhanced hydrogen sulfide production, alongside upregulating the expression levels of genes encoding SUMO E3 ligase SIZ1 and HEAT SHOCK PROTEINS (HSPs) 70/90 (Aghdam and Flores, 2021; Aghdam et al., 2021a). On the other side, PSK peptides

decrease the activities of phospholipase D and lipoxygenase, thus reducing endogenous hydrogen peroxide (H_2O_2) accumulation and protecting membrane integrity featured as lower malondialdehyde accumulation, all of which collectively delays senescence in broccoli florets (Aghdam and Flores, 2021). Similarly, PSK application delays petal senescence in cut rose (*Rosa hybrida* cv. 'Angelina') flowers by potentiating SUMO1/SUMO E3 ligase SIZ1 signaling and suppressing endogenous H_2O_2 accumulation (Aghdam et al., 2021b). In litchi (*Litchi chinensis* Sonn. cv. 'Guiwei'), PSK peptide application has also been shown to effectively impede litchi pericarp browning by modulating oxidative enzymatic reactions and suppressing the expression of browning-related genes (Liang et al., 2025). A recent genetic and molecular study demonstrated that the exogenous application of sulfated, mature PSK peptide facilitates fruit color transition, ripening, and quality establishment of tomato (*Solanum lycopersicum* L. cv. 'Condine Red') fruits by inducing phosphorylation of the transcription factor DEHYDRATION-RESPONSIVE ELEMENT BINDING PROTEIN 2F (DREB2F) via the PSK RECEPTOR 1 (PSKR1)

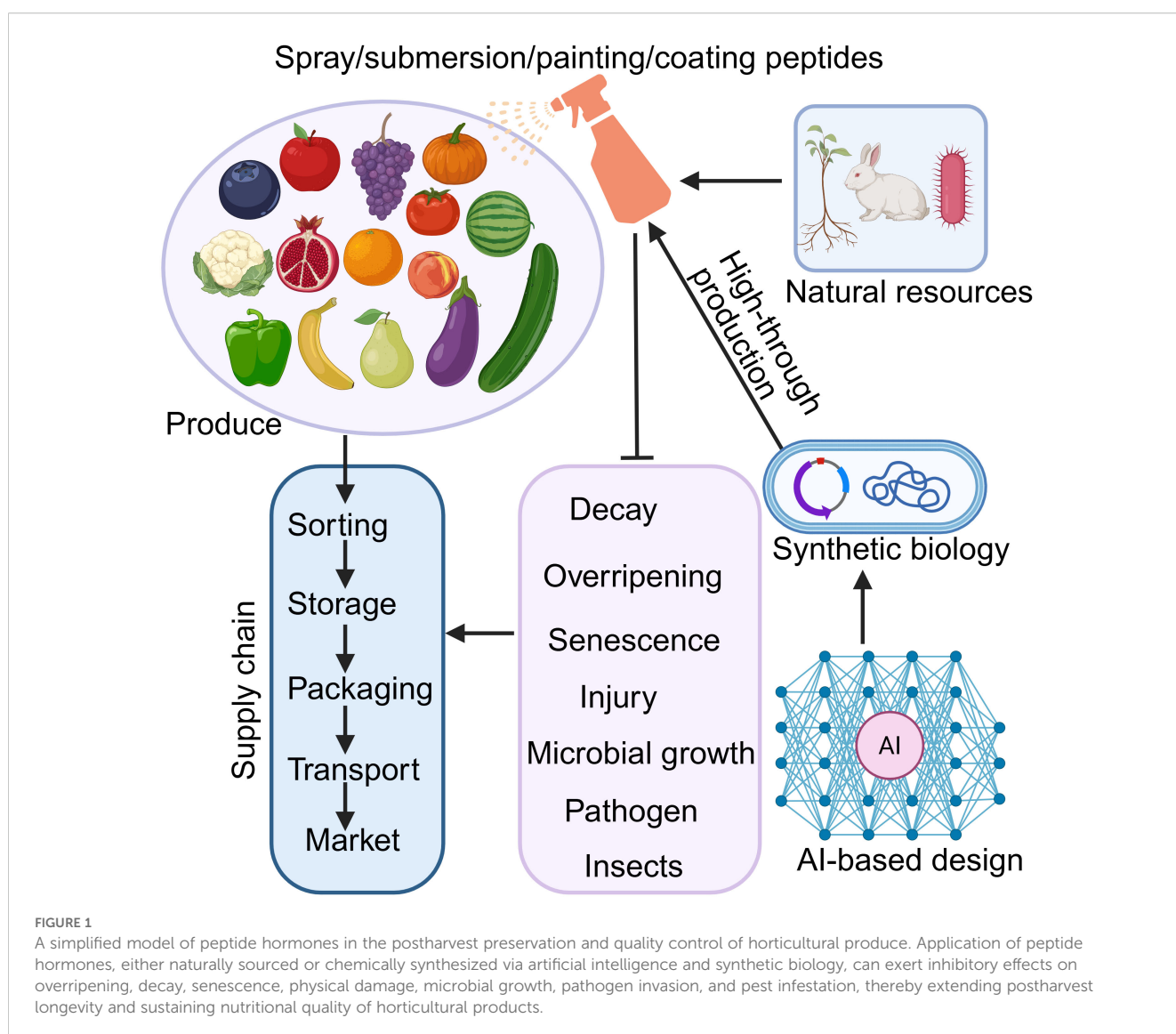


TABLE 1 A summary of peptide hormones in postharvest preservation.

Peptides	Plant species	Function	Downstream signaling	Reference
RGFGLV (CTG134 peptide)	Peach	Ripening	Auxin and ethylene	Tadiello et al., 2016
PSK	Peach	Cold tolerance	ROS and cell wall metabolisms	Zeng et al., 2024
PSK	Broccoli	Delay yellowing and preserve the nutritional integrity under cold	cGMP, phenols, flavonoids, and ascorbic acid	Aghdama et al., 2020
PSK	Broccoli	delays senescence	Phospholipase D, lipoxygenase, H ₂ O ₂	Aghdam and Flores, 2021
PSK	Rose	Delay petal senescence	H ₂ O ₂	Aghdam et al., 2021b
PSK	Tomato	Fruit ripening	DREB2F	Fang et al., 2024
PSK	Loquat	Chilling tolerance	Energy status and cell integrity	Song et al., 2017
PSK	Bananas	Chilling injury	Nitric oxide, polyamine, proline, and γ-Aminobutyric	Wang et al., 2022
PSK	Strawberry	Relieve fungal decay, delay senescence	ROS, ATP	Aghdam and Alikhani-Koupaei, 2021; Aghdam et al., 2021c, 2021
RALF33	Strawberry	Anthrachnose ontogenic resistance		Merino et al., 2019

receptor (Fang et al., 2024). Importantly, peptide hormones exhibit high binding affinities, high selectivity and specificity, and good efficacy in their actions (Ji et al., 2025; Zhang et al., 2025), thereby avoiding non-specific, side, or off-target adverse effects. High functional specificity and binding affinity of peptide hormones also contribute to their favorable safety profile and low frequency of off-target effects. Their general hydrophilicity further reduces the potential for tissue accumulation. Furthermore, peptide hormones are typically degraded into non-toxic metabolites (amino acids). Moreover, since peptide hormones derived from plant sources offer an environmentally safe way for regulating fruit and vegetable production without causing environmental pollution. Taken together, these studies demonstrate that, acting as function-specific, good efficacy, safer, and environmentally friendly alternatives, peptide hormones play curial roles in delaying senescence, extending shelf life, and maintaining fruit quality during postharvest preservation (Table 1).

Peptide hormones are also known to play roles in response to abiotic stress and pathogenic invasions (Wang et al., 2016; Ji et al., 2025; Zhang et al., 2025), underscoring their potential to alleviate adverse conditions and infectious diseases in fruits and vegetables during postharvest preservation (Figure 1). In loquat (*Eriobotrya japonica* (Thunb.) Lindl. cv. ‘Luoyangqing’) fruits, a cold-induced PSK peptide PSK1 was found to improve chilling tolerance of loquat fruit by sustaining high energy status and cell integrity, exhibiting retardation of internal browning development and weight loss in PSK1-treated fruits (Song et al., 2017). Furthermore, exogenous application of PSK peptides also confer tolerance to chilling injury, thus repressing internal browning, delaying senescence, and preserving nutritional quality of loquat (*Eriobotrya japonica* Lindl. cv. ‘Jiefangzhong’) fruits during cold storage (Liu et al.,

2024). Mechanistically, PSK peptide alleviates chilling injury and maintains fruit quality during of loquat during cold storage, which is achieved by regulating the metabolism of sugar, proline, polyamines, and γ-aminobutyric acid (Liu et al., 2024). In bananas (*Musa acuminata* cv. ‘Brazil’), PSK application similarly mitigates chilling injury, such as cold-induced browning and water-soaking by regulating nitric oxide, polyamine, proline, and γ-aminobutyric acid metabolisms (Wang et al., 2022). PSK treatment also can delay and alleviate the flesh browning caused by chilling injury, thereby preserving quality and flavor of postharvest peach (*Prunus persica* (L.) Batsch. cv. ‘Hujingmilu’) fruit via modulating ROS and cell wall metabolisms (Zeng et al., 2024). Beyond abiotic stress, exogenously applied of PSK peptides have been shown to relieve fungal decay and delay senescence in strawberry (*Fragaria × anannasa* cv. ‘Selva’ and ‘Camarosa’) fruits through activating extracellular ATP signaling, improving REACTIVE OXYGEN SPECIES (ROS) scavenging, and promoting antioxidant nutrient accumulation during cold storage (Aghdam and Alikhani-Koupaei, 2021; Aghdam et al., 2021c, 2021). In addition, the RAPID ALKALINIZATION FACTOR 33 (RALF33) peptide has been shown to negatively regulate anthracnose ontogenic resistance in unripe strawberry (*Fragaria × ananassa* cv. ‘Alba’) fruits (Merino et al., 2019). Altogether, these findings demonstrate that small signaling peptides are able to combat both abiotic and biotic stresses during postharvest preservation, leading to prolonged storage duration and improved quality of fruits and vegetables (Table 1). Given that many peptide hormones are heavily implicated in stress acclimatization (Wang et al., 2016; Ji et al., 2025; Zhang et al., 2025), it is expected that additional peptide hormones could be assigned with roles in postharvest preservation of fruits and vegetables.

Future challenges and perspectives

Despite their considerable potential, the full utilization of small signaling peptides in postharvest preservation is constrained by several limitations, including poor stability, limited bioavailability, inefficient delivery into target tissues, and high production costs. Consequently, future peptide production must prioritize high stability, low cost, and safety. Artificial Intelligence (AI) and synthetic biology represent promising methodologies for next-generation peptide production, enabling enhanced stability, optimized formulations, and enable cost-effective, high-throughput manufacturing (Figure 1). For instance, the AI-based design of antiproteolysis peptide, APP3-14, has been demonstrated to control Huanglongbing, a catastrophic disease affecting citrus crops (Zhao et al., 2025). By integrating deep learning algorithms, Zhao et al. (2025) efficiently identified a series of therapeutic peptides, including APP3-14 which significantly inhibits the colonization of the Huanglongbing pathogen and disrupt its transmission cycle. In this context, a couple of successful AI platforms and tools, for instance, AlphaFold-Multimer, neural language models (NLMs), variational autoencoders (VAEs), generative adversarial networks (GANs), and the PepINVENT tool can be applied to design novel small peptides for horticultural produce preservation (Wan et al., 2022; Geylan et al., 2025). As such, the AI-aided improved stability, low toxicity, and enhanced functional specificity of peptide hormones offer environment-friendly alternatives for postharvest longevity.

Over 30 families of peptide hormones were identified across plant species (Zhang et al., 2025), whereas only a few have been characterized for postharvest preservation roles. Given that many peptide hormones are involved in response to senescence, chilling stress, and pathogen diseases that frequently occur during postharvest storage, further exploration is expected to reveal additional peptide hormones with functions in postharvest management of fruits and vegetables. Preharvest interventions are equally critical; thus, it is very likely that applying peptide hormones could preempt latent infections or reinforce prepared cellular integrity. Peptide hormones can be exogenously applied via sprays, submersion, painting, and coating (Figure 1). Peptide hormones regulate key agronomic and horticultural traits that significantly influence the postharvest quality of fruits and vegetables (Ji et al., 2025; Zhang et al., 2025). In this regard, beyond exogenous application, gene editing or genetic transformation offers a promising avenue to modulate endogenous peptide levels, thereby harnessing their innate antimicrobial, antioxidative, and anti-aging properties to sustain quality and extend storage duration. Consequently, genetic improvement targeting functional peptide-encoding genes represents a fundamental strategy for addressing postharvest challenges in horticultural crops.

Importantly, peptide hormone-based composite materials can integrate multiple functional advantages to reduce postharvest losses. For instance, combining peptides with nanoparticles, polysaccharides, polyphenols, or nutrients can yield edible composites that simultaneously maintain quality and enhance nutritional value (Ranjith et al., 2022; Tkaczewska, 2020). Furthermore, peptide hormones can be synergistically combined

with other preservation techniques, such as cold storage, modified atmosphere packaging, and edible coatings, to leverage complementary advantages and improve overall preservation efficacy.

In conclusion, despite significant challenges, ongoing technological advances and research efforts are poised to expand the application of peptide hormones in mitigating postharvest losses. By ensuring stability, safety, and cost-efficiency, peptide hormone-based strategies can contribute significantly to the sustainable development of the horticultural industry.

Author contributions

JN: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. HB: Writing – review & editing. SJ: Writing – review & editing. HH: Writing – review & editing, Conceptualization, Funding acquisition. GW: Conceptualization, Funding acquisition, Writing – review & editing, Writing – original draft.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. This work is supported by National Natural Science Foundation of China (32370850, 32460081), Leading Talent of Technological Innovation of Shaanxi Special Support Program (20249), Key Project of the Natural Science Foundation of Shaanxi (2023-JC-ZD-09), China Postdoctoral Science Foundation (2025M773739), Shaanxi Postdoctoral Research Project (2024BSHSDZZ183), Natural Science Foundation of Shaanxi for Distinguished Young Scholars (2020JC-29), and Fundamental Research Funds for the Central Universities (GK202402003; GK202506006).

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