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Glucosinolates and their hydrolysis products as a sustainable strategy in the control of postharvest diseases in non-Brassicaceae fruits and vegetables

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ABSTRACT

Postharvest losses in fruits and vegetables represent a critical challenge for global food security and sustainability, accounting for up to 28–55 % of total production in some regions. Conventional control strategies, largely based on synthetic fungicides and physical treatments, face increasing limitations due to concerns over resistance development, chemical residues and environmental impact. This review provides a comprehensive analysis of glucosinolates (GSLs) and their hydrolysis products (GHPs) as promising biocidal agents for the management of postharvest diseases in non-Brassicaceae fresh produce. We summarize current knowledge on the chemical nature, biosynthesis and hydrolytic activation of GSLs, as well as their mechanisms of action against key postharvest pathogens, including fungi, oomycetes and bacteria. Furthermore, we critically examine application strategies—such as biofumigation, plant extracts, volatile release, and the use of commercial or modified GHPs—along with their reported efficacy in *in vitro* and *in vivo* studies. The review highlights knowledge gaps related to mechanistic understanding, formulation stability, and industrial scalability, outlining future research directions to translate these compounds into sustainable and commercially viable solutions for reducing postharvest losses.

1. Introduction

Fresh fruits and vegetables are among the most widely cultivated and consumed agricultural commodities worldwide. Their high nutritional value, rich content of bioactive compounds, and increasing consumer preference for healthy diets have driven a steady growth in their production and commercialization (FAO, 2024a). In 2023, global fruit and vegetable production surpassed 2.1 billion tons, a 30 % increase since 2010, representing a growing multi-billion-dollar industry with significant economic impact, particularly in developing countries where these products contribute substantially to food security and income generation (FAO, 2024a).

However, the high perishability of fresh produce may produce huge losses during harvest, postharvest handling, storage, packaging and distribution (Al-Dairi et al., 2022). Postharvest losses, caused by mechanical damage, pests and microbial pathogens, are responsible for considerable qualitative and quantitative losses across the supply chain (Singh et al., 2021). It is estimated that postharvest losses of fruits and vegetables may reach 28–55 % in certain regions, particularly in developing areas, such as sub-Saharan Africa, where deficiencies in cold-chain infrastructure and limited implementation of effective disease management strategies exacerbate the problem (FAO, 2019, 2024b). The annual economic value of these losses accounts for approximately USD 750 billion, which represents a critical challenge for the global agricultural production sector (Karoney et al., 2024). These losses translate not only into economic setbacks for producers, retailers and consumers, but also into serious environmental implications due to resource waste (land, water, fertilizers, labour and energy). In high-income countries, although losses are generally lower, significant investments are made in postharvest disease control using synthetic fungicides, sanitizing agents and advanced packaging technologies, often with limited long-term sustainability (Yahia et al., 2019). The United Nations (UN), in the framework of the Sustainable Development Goals (SDGs), set in 2015 the objective of reducing food losses and waste

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Table 1
Main postharvest pathogens in non-Brassicaceae fruits and vegetables, associated diseases, and reported extent of damage.

GROUP	PATHOGEN(S)	AFFECTED CROP(S)	DISEASE	REPORTED EXTENT OF DAMAGE	REFERENCES
Fungi	*Botrytis cinerea*	Tomato, cucumber, grape, strawberry, apple, tubers	Gray mold	>1 billion USD in global annual losses	Zhang et al. (2021)
	Penicillium digitatum, *P. italicum*	Citrus	Green and blue mold	Major contributors to global postharvest citrus losses	Chen et al. (2023); Karoney et al. (2024)
	Penicillium expansum	Apple, pear, grape	Blue mold	Significant economic losses + patulin production (food safety risk)	Li et al. (2024a)
	Colletotrichum spp.	Mango, papaya, banana, avocado	Anthracnose	Relevant postharvest losses in tropical crops (no global % available)	Karoney et al. (2024)
	Alternaria spp.	Tomato, pepper, brassicas	Black rot	Frequent damage during storage and marketing	Chen et al. (2023)
	Aspergillus spp.	Grape, fig	"Bird's eye rot" and rots	Economic losses + mycotoxin contamination	Wenneker and Thomma (2020)
Oomycetes	*Phytophthora infestans*, *P. capsici*	Potato, tomato, pepper, cucumber, eggplant, tobacco	Late blight, fruit rot	>100 million USD in annual losses	Barchenger et al. (2018); Kousik et al. (2022)
	Phytophthora citrophthora, *P. parasitica*	Citrus	Brown rot	Major postharvest citrus disease	Fadli et al. (2022)
	Pythium ultimum, *P. aphanidermatum*	Cucumber, pumpkin, melon	Soft rot	Significant storage and transport losses	Singh and Afaque (2021)
Bacteria	*Pectobacterium* spp., *Dickeya* spp.	Potato, carrot, cucumber, tomato	Soft rot	Leading cause of bacterial postharvest losses in vegetables	FAO, 2023
	Xanthomonas spp., *Pseudomonas* spp.	Lettuce, cabbage, pepper, tomato	Watery lesions, rots	Quality losses (watery lesions, tissue breakdown, discoloration)	Kamboj et al. (2021)
	Burkholderia cepacia, *Ralstonia* spp.	Onion, root crops	Emerging rots	Identified as emerging postharvest pathogens	Kamboj et al. (2021)
	Salmonella enterica, *Listeria monocytogenes*, pathogenic *E. coli*	Melon, papaya, spinach, romaine lettuce	Contamination, foodborne disease	Major outbreaks of foodborne illness	Zhu et al. (2017)

by 50 % by 2030 (UN, 2015), however, according to recent FAO and UN reports the effort made is insufficient: food losses and waste have not been reduced since at least 2016 (FAO, 2021; UNEP, 2021). In this context, more efforts are needed, both globally and locally, to face this challenge.

Various strategies, including cold storage, controlled atmosphere packaging, and chemical treatments, have been employed to mitigate postharvest losses (Karoney et al., 2024). However, these studies have focus mainly on cereals and on the farm level, and not all these strategies and studies have been successful (Stathers et al., 2020). Some postharvest treatments may also affect nutritional properties of the fresh produce (Moradinezhad and Ranjbar, 2023). Chemical treatments are globally adopted in reducing fruits and vegetables postharvest losses, however the growing concerns over chemical residues, antimicrobial resistance and the environmental impact of conventional methods have sparked interest in developing alternative strategies for postharvest disease control. In this context, biological control with microorganisms and natural compounds derived from plants—particularly secondary metabolites with antimicrobial activity—are gaining attention as promising, eco-friendly tools (Wan et al., 2021; Li et al., 2024a). Among them, glucosinolates (GSLs) and their hydrolysis products (GHPs) stand out due to their well-documented roles in plant defense and their potential biocidal properties (Eugui et al., 2023, 2025).

This review aims to provide a comprehensive overview of postharvest diseases affecting fresh produce and current control strategies, with a special focus on the use of GSLs and GHPs as efficients biocontrol tools. We will explore their chemical nature, biological activity, modes of action and potential applications in postharvest disease management, highlighting both opportunities and research gaps that must be addressed to translate these natural compounds into practical, effective solutions.

2. Postharvest diseases of fresh produce

Postharvest diseases of fresh produce are primarily caused by microbial pathogens that exploit physiological vulnerabilities in plant tissues during or after harvest (Table 1). Among these, fungi represent the most significant threat, particularly due to their ability to establish quiescent or latent infections during fruit development and remain asymptomatic until postharvest conditions favor their activation. While most postharvest pathogens are necrotrophic fungi, drawing nutrients from death host cells (Li et al., 2024a), these pathogens typically initiate biotrophic interactions—obtaining nutrients from living host cells—before transitioning to a necrotrophic lifestyle, characterized by host cell death and visible decay symptoms during ripening and senescence (Perfect et al., 1999; Prusky and Lichter, 2007). Fungal pathogens employ multiple infection routes, including penetration through wounds, natural openings such as lenticels or stem ends, or direct cuticle breach, which usually occur during farm and market labors (e.g., transport, packaging). Although viruses may play a role in a few postharvest disorders, especially in some root vegetables and brassicas, they are not considered major contributors to postharvest decay (Coates and Johnson, 1997). This section will explore the key pathogen groups—fungi, bacteria, and oomycetes—that contribute to postharvest losses, emphasizing their infection biology, host interactions, and impact on fresh produce quality.

Fungi are responsible for the majority of postharvest diseases affecting fresh produce, posing a significant threat to global food quality and security. Among the most important fungal pathogens are species of *Botrytis* (gray mold), *Alternaria* (black rot), *Penicillium* (blue and green molds), *Colletotrichum* (anthracnose) and *Aspergillus* (bird's eye rot), all of which infect a wide variety of fruits and vegetables across diverse climatic regions and supply chains (Chen et al., 2023; Karoney et al., 2024; Li et al., 2024a). Moreover, emerging fungal pathogens and novel postharvest diseases are continually being identified, reflecting the dynamic nature of host–pathogen interactions and the ongoing need for updated surveillance and control strategies (Wenneker and Thomma, 2020). Given the broad host range and increasing complexity of postharvest fungal infections, it is crucial to consider the specific crops most severely affected and their economic implications. While specific data on fungal-induced postharvest losses are scarce, *Botrytis cinerea* alone causes annual losses globally in many horticultural crops such as tomato, cucumber, grapes, strawberries, apples or tubers, causes over a billion USD of global losses every year (Zhang et al., 2021). In addition to causing economic losses through spoilage, several postharvest fungi can synthesize mycotoxins, which represent a major risk to human health (Liu et al., 2020).

In addition to fungi, oomycetes also cause important loses in fresh produce supply chain, being the most prevalent oomycete genus *Phytophthora* and *Pythium* (Coates and Johnson, 1997; Yu et al., 2023). *Phytophthora* genus has a wide range of hosts. *P. infestans* and *P. capsici* cause annual losses over 100 million USD in cucurbits and solanaceous crops, such as cucumber, potato, tomato, pepper, eggplant or tobacco (Barchenger et al., 2018; Kousik et al., 2022), while *P. citrophthora* and *P. parasitica* cause the brown rot in citrus (Fadli et al., 2022). On the other hand, *P. ultimum* and *P. aphanidermatum* cause soft rot in cucurbits, contributing to significant postharvest losses in crops such as cucumber, pumpkin or melon (Singh and Afaque, 2021).

Although fungal pathogens are the predominant cause of postharvest decay, bacterial pathogens also contribute significantly to quality losses and food safety concerns in fresh produce. Bacterial postharvest infections are usually related to pH condition of the fresh produce. Acidity is often inhibitory to these pathogen group but vegetables, with generally a higher pH than fruits, tend to be more susceptible to bacteria (Antunes and Cavaco, 2010). Bacterial postharvest infections usually cause soft rots in a wide range of hosts during storage and transportation. A wide range of bacterial pathogens have been described from diverse genera, such as *Pectobacterium*, *Bacillus*, *Enterobacter*, *Pseudomonas* or *Klebsiella* (Yi et al., 2021; Li et al., 2024b). Among the most important postharvest bacterial genera are *Pectobacterium* and *Dickeya* (formerly grouped under *Erwinia*), responsible for soft rot diseases in vegetables such as potato, carrot, cucumber, and tomato (FAO, 2023). *Xanthomonas* and *Pseudomonas* species are also frequently implicated in spoilage, causing watery lesions, tissue breakdown, and discoloration in crops like lettuce, cabbage, pepper, and tomato (Kamboj et al., 2021). Additionally, *Burkholderia cepacia* and *Ralstonia* spp. have been identified as emerging postharvest pathogens in onion and other root crops. Beyond spoilage, certain bacteria—particularly *Salmonella enterica*, *Listeria monocytogenes*, and pathogenic *Escherichia coli* strains—pose serious risks of foodborne illness through contamination of fresh-cut fruits (e.g., melon, papaya) and leafy greens (e.g., spinach, romaine lettuce) (Zhu et al., 2017). These bacterial infections, while often less visible than fungal rots, are a critical component of postharvest pathology due to their capacity to rapidly proliferate under storage and transport conditions and compromise both shelf-life and consumer health.

3. Strategies for the control of postharvest diseases in fresh produce

The management of postharvest diseases in fresh produce relies on a combination of physical, chemical and biological approaches, each with distinct mechanisms and degrees of efficacy. Effective postharvest disease management begins in the field through strategies aimed at minimizing fruit wounding by using appropriate harvesting and handling equipment, as well as reducing pathogen inoculum levels prior to harvest. Ensuring the microbiological quality of irrigation water is also essential, particularly in the case of leafy vegetables, where contamination risks are high (Gil et al., 2015). After harvest, regular inspections and detection systems are key factors in reducing postharvest losses, but its use is mostly restricted to developed countries (Habib and Rizk, 2021). Physical methods are broadly adapted and include cleaning and washing the fresh produce, temperature control (cold storage, heat treatments), modified atmosphere packaging or irradiation. These techniques are widely applied to delay microbial growth and extend shelf life, although they may be costly or impractical in some production contexts. Chemical control, predominantly through synthetic fungicides, has long been the cornerstone of postharvest disease management. Compounds, such as thiabendazole, imazalil or fludioxonil, are commonly used to control decay caused by pathogens like *Penicillium*, *Botrytis* and *Colletotrichum* (Chen et al., 2021). However, increasing concerns over fungicide resistance, environmental toxicity and residue limits have driven the search for alternative strategies (D'Aquino et al., 2013). As reliance on chemical fungicides becomes increasingly unsustainable, attention has shifted toward safer, biologically based methods and the exploitation of natural and biological resources.

In this context, biological control and the use of plant-derived compounds have emerged as promising and sustainable alternatives. Antagonistic microorganisms such as *Bacillus*, *Pseudomonas* and various yeasts, have been explored for their ability to outcompete or inhibit fungal and bacterial pathogens (Droby et al., 2009; Sharma et al., 2009; Hosseini et al., 2024). Moreover, considerable attention has been devoted to plant extracts and essential oils, which contain natural antimicrobial compounds such as phenolics, flavonoids, alkaloids and GSLs (Eugui et al., 2025; Flores and Poveda, 2025). These substances act through multiple mechanisms—disrupting microbial membranes, inhibiting spore germination, or interfering with pathogen metabolism—and are often biodegradable and low in toxicity (Sellamuthu et al., 2013). Plant-based extracts, especially those from species in the Brassicaceae, Lamiaceae and Rutaceae families, have shown promising *in vitro* and *in vivo* efficacy against key postharvest pathogens. While challenges remain regarding formulation stability, regulatory approval and large-scale application, plant-derived compounds represent a central axis in the development of next-generation, eco-friendly postharvest treatments. Within the wide spectrum of natural metabolites, GSLs represent a distinctive class of sulfur- and nitrogen-containing compounds whose antimicrobial potential extends beyond their natural role in Brassicaceae defense. Recent advances suggest that GSLs and their hydrolysis products may be harnessed as sustainable tools in postharvest disease control, complementing or even enhancing existing biological and chemical approaches.

4. Glucosinolates (GSLs): plant defense metabolites

GSLs are sulfur- and nitrogen-containing secondary metabolites predominantly found in plants of the Brassicaceae family, including economically and nutritionally important species such as broccoli, cabbage, mustard and radish (Šamec et al., 2017). These compounds are not directly toxic in their intact form but are enzymatically hydrolyzed by the enzyme myrosinase into biologically active products—GHPs—such as isothiocyanates (ITCs), nitriles, thiocyanates, and epithionitriles (Wu et al., 2021). In the plant, GSLs function primarily in defense, deterring herbivores and pathogens while also playing regulatory roles in development and response to abiotic stresses (Hossain et al., 2013; Martínez-Ballesta et al., 2014; Jensen et al., 2015; Vik et al., 2018). From a human perspective, GSLs and their hydrolysis products have attracted considerable interest due to their antioxidant, anti-inflammatory, antimicrobial and anticancer properties, reinforcing the importance of Brassicaceae crops in both health-promoting diets and integrated pest management strategies (Poveda et al., 2020; Li et al., 2022).

There are over 130 distinct GSLs identified, which are typically classified based on their amino acid precursors into three groups: aliphatic (derived from methionine, alanine, etc.), indolic (from tryptophan) and aromatic (from phenylalanine or tyrosine) (Clarke, 2010; Lee et al., 2012). Their biosynthesis is a complex process involving three main phases: chain elongation of the amino acid precursor, core structure formation, and side-chain modifications (Nintemann et al., 2018). Transport of GSLs occurs via specific GSL transporters (GTRs) that mediate their distribution throughout the plant, including relocation to damaged or infected tissues (Blažević et al., 2020). This dynamic regulation and distribution are crucial to their defensive role, as GSLs can be mobilized quickly to sites of pathogen attack (Poveda et al., 2020).

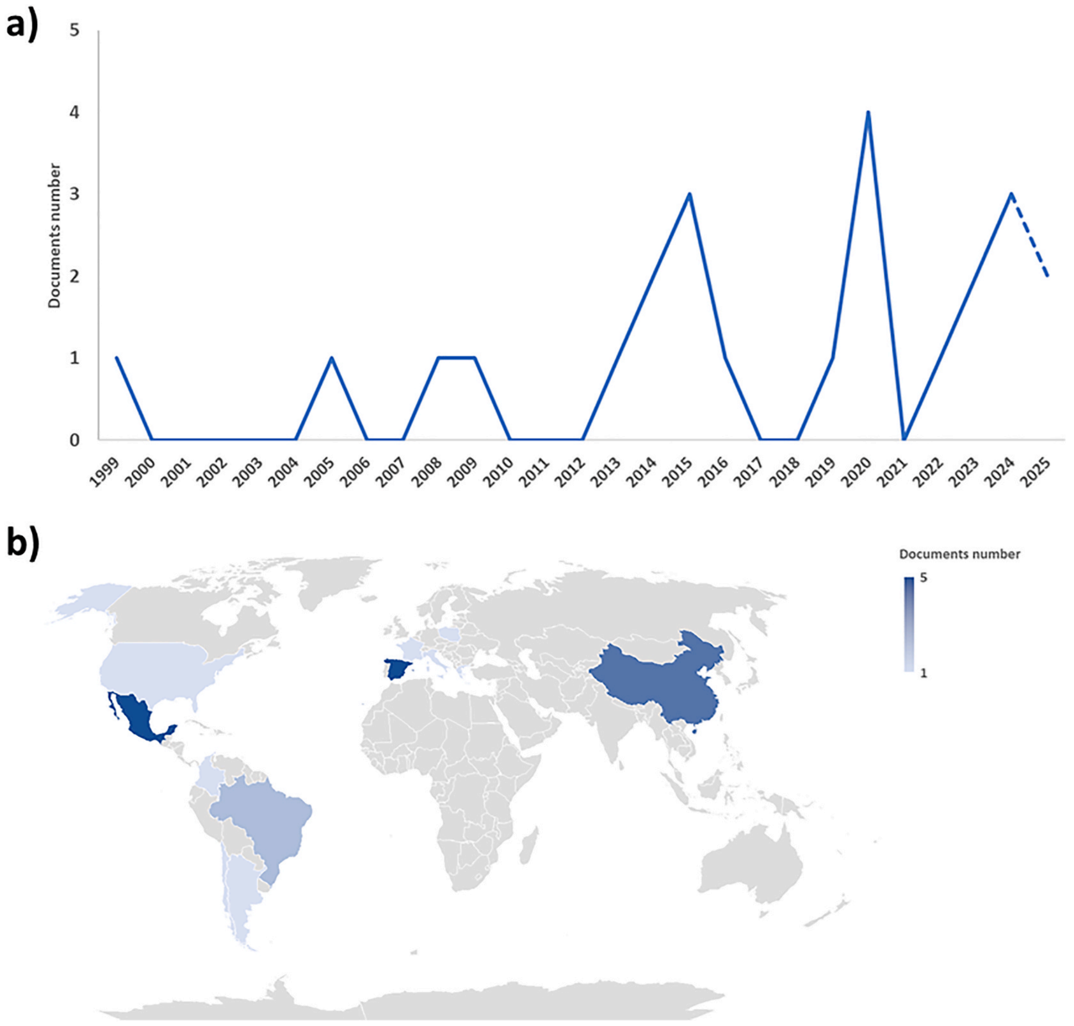

Fig. 1. Graphical representation of the data obtained in the bibliographic search. Number of articles per year (a) and countries of authors (b), the legend represents the number of articles per country. As only articles published in the year 2025 up to the month of June have been analyzed, this year appears with a dotted line (a).

4.1. GSLs and GHPs as biocides in plant health

Due to the bioactivity of their hydrolysis products, GSLs have gained attention as biocidal agents against a broad spectrum of plant pathogens and pests. Application strategies include incorporation of Brassicaceae residues into soil (biofumigation), use of Brassicaceae seed meals, purified GSLs or GSL-rich extracts, or co-application with the myrosinase enzyme to ensure *in situ* hydrolysis to active compounds (Gimsing and Kirkegaard, 2009; Poveda et al., 2020; Eugui et al., 2022). Recent research has focused on scaling up extraction protocols from agricultural residues, such as broccoli leaves, to produce efficient, stable, and cost-effective biopesticides (Eugui et al., 2023).

4.1.1. Antifungal activity

GSLs and their hydrolysis products, particularly ITCs, have demonstrated antifungal and anti-oomycete activity through multiple mechanisms. These include disruption of cell membranes, induction of oxidative stress via ROS accumulation, mitochondrial dysfunction, and inhibition of fungal growth and sporulation (Calmes et al., 2015; Murata et al., 2019). GSLs and GHPs have been extensively investigated for their capacity to suppress fungal pathogens and mitigate disease incidence across diverse cropping systems. Their efficacy has been demonstrated against soilborne pathogens such as *Verticillium dahliae* (Neubauer et al., 2014, 2015), *Fusarium oxysporum* (Villalta et al., 2016; Ren et al., 2018), *Sclerotinia sclerotiorum* (Abuyusuf et al., 2018; Madloo et al., 2019) or *Rhizoctonia solani* (Handiseni et al., 2013, 2016; Villalta et al., 2016), as well as against aerial and postharvest pathogens including *Alternaria alternata* (Flores-Córdova et al., 2013; Wang et al., 2020; Zhang et al., 2020), *B. cinerea* (Ugolini et al., 2014), *Penicillium expansum* (Manyes et al., 2015), *Aspergillus parasiticus* (Manyes et al., 2015) or *Colletotrichum gloeosporioides* (Lara-Viveros et al., 2014).

4.1.2. Anti-oomycete activity

In contrast to fungi, the impact of GSLs and GHPs on plant-pathogenic oomycetes has received comparatively less attention. Existing research has primarily focused on species of the genus *Pythium* and *Phytophthora* (Ren et al., 2018), such as *P. ultimum* (Handiseni et al., 2012), *P. spiculum* (Arroyo-Cordero et al., 2019) or *Phytophthora cinnamomi* (Ríos et al., 2017; Arroyo-Cordero et al., 2019). Notably, some studies have reported antagonistic outcomes, wherein GSL application resulted in increased oomycete populations rather than suppression, highlighting the importance of extract formulation and application context (Cohen and Mazzola, 2006; Mazzola et al., 2007; Eugui et al., 2023).

4.1.3. Antibacterial activity

In the case of bacterial pathogens, studies have shown that certain GHPs, especially ITCs, can inhibit bacterial growth through membrane damage, interference with sulfur metabolism, and inhibition of key enzymatic systems (Borges et al., 2015). While the antibacterial activity of GSLs is generally less potent than against fungi, several studies indicate they are related to certain *Brassica* enhanced resistance mechanisms and can reduce populations of plant pathogenic bacteria, such as *Pectobacterium brasiliense* (Yi et al., 2022), *Erwinia carotovora* (Tierens et al., 2001), *Pseudomonas syringae* (Tierens et al., 2001; Sotelo et al., 2015) or *Xanthomonas campestris* (Tierens et al., 2001; Sotelo et al., 2015; Madloo et al., 2019).

4.1.4. Nematicidal activity

GSLs and their hydrolysis products also exhibit nematicidal activity. The primary mechanism involves the toxicity of ITCs, which disrupt neuromuscular function and induce mortality in juvenile stages (Wu et al., 2014; Aissani and Sebai, 2022). The GSLs and GHPs can also inhibit egg hatching and reduce reproductive ability after exposure (Ntalli and Caboni, 2017; Tarini et al., 2020; Eugui et al., 2023). Additionally, indirect mechanisms, such as stimulation of soil microbial communities that compete with or antagonize plant-parasitic nematodes (PPNs), contribute to their efficacy (Gimsing and Kirkegaard, 2009).

Given the broad antimicrobial spectrum and varied mechanisms of action associated with GSLs and their hydrolysis products, the following section explores in greater depth the current body of research on their application for postharvest disease control in fruits and vegetables, including experimental strategies and delivery approaches.

5. Analysis conducted

A literature review was performed together with a quantitative analysis of publications according to year, journal and countries. The compilation of all publications was done with the keywords “glucosinolates AND postharvest AND fruit OR vegetable AND disease OR pathogen AND protection”. The bibliographic database Web of Science™ (Web of Science Core Collection - WoS) (https://www.webofscience.com) and the Elsevier® Scopus library services metabase (https://www.scopus.com) were used, due to the advantages of scientific rigor compared to other free and more open databases, such as Google Scholar (Martín-Martín et al., 2021).

In WoS, after searching for keywords in “All fields”, without time restriction, and by selecting the document type “articles”, 58,469 results were retrieved (search performed on June 26, 2025). Of these 58,469 articles, 58,448 were not related to the subject, therefore, 21 articles were included in the review. On the other hand, in Scopus, after searching for keywords in “All fields”, without time restriction and by selecting the document type “articles”, 384 results were retrieved in Scopus (search performed on June 26, 2025), of which 360 were not related to the subject of this work, therefore, 24 articles were included in the review. It is important to note the overlapping results between the two databases. Of the 21 articles used from WoS and the 24 from Scopus, 21 match, contributing 3 unique articles from Scopus. Therefore, the total number of final articles of the review on the use of GSLs and GHPs for the control of postharvest diseases in non-Brassicaceae fruits and vegetables, was 24 articles.

The first publication on this topic was published in 1999 (Olivier et al., 1999), with intermittent publications until 2013 (Troncoso et al., 2005; Mari et al., 2008; Troncoso-Rojas et al., 2009). Subsequently, between 2013 and 2025, most publications on the subject were produced. There were peaks in the number of publications in 2020 (four articles), 2015 and 2024 (three articles), as well as an absence of publications in 2017, 2018 and 2021 (Fig. 1a).

With regard to the country of affiliation of the authors of the articles, Mexico and Spain were the countries with the most articles, with 5. Next in importance was China, with 4 articles, and Brazil, with 2 articles. Additionally, single publications were identified in 11 other countries across Asia (Turkey), the Americas (Argentina, Chile, Colombia and USA) and Europe (France, Greece, Italy and Poland) (Fig. 1b).

These authors published their articles in 21 different journals, including *Scientia Horticulturae* (with 3 articles) and *Plant Protection Science* (with 2 articles). The remaining journals published only one article (Table 2). In terms of the number of citations received by these articles, the one published in the journal *Applied and Environmental Microbiology* in 2015 (Sotelo et al., 2015) stands out, with 97 citations in WoS and 104 in Scopus. In second place is an article published in 1999 in the journal *Journal of Chemical Ecology* (Olivier et al., 1999), with 96 (Scopus) and 80 (WoS) citations, and another published in 2005 in the journal *Food Research International* (Troncoso et al., 2005), with 80 in WoS and 96 in Scopus. Only one article less than 5 years old ranked

Table 2
Journals where the reviewed papers were published.

JOURNAL	NUMBER OF ARTICLES	PAPERS REFERENCES
Scientia Horticulturae	3	Pazolini et al. (2016); Koltz et al. (2020); Damas-Job et al. (2023)
Plant Protection Science	2	Arroyo-Cordero et al. (2019); Kowalska et al. (2025)
Applied and Environmental Microbiology	1	Sotelo et al. (2015)
Biagro	1	Sánchez-León et al. (2015)
Biomolecules	1	He et al. (2024)
Combinatorial Chemistry & High Throughput Screening	1	Stegmayer et al. (2022)
Food Research International	1	Troncoso et al. (2005)
Industrial Crops & Products	1	Eugui et al. (2023)
International Journal of Food Microbiology	1	Dagnas et al. (2015)
International Journal of Molecular Sciences	1	Román et al. (2024)
Journal of Agricultural and Food Chemistry	1	Wang et al. (2024)
Journal of Chemical Ecology	1	Olivier et al. (1999)
Journal of Phytopathology	1	Kara and Soylu (2020)
Journal of Plant Diseases and Protection	1	Eugui et al. (2025)
Molecules	1	Velasco et al. (2013)
Phytoparasitica	1	Troncoso-Rojas et al. (2009)
Plant Disease	1	Ren et al. (2020)
Postharvest Biology and Technology	1	Mari et al. (2008)
Revista Chapingo Serie Horticultura	1	Flores-Córdova et al. (2014)
Revista Fitotecnia Mexicana	1	Lara-Viveros et al. (2014)
RSC Advances	1	Wang et al. (2020)

Table 3
Number of citations of the 10 most cited articles.

RANKING	REFERENCE	JOURNAL	WoS CITATIONS	Scopus CITATIONS
1	Sotelo et al. (2015)	*Applied and Environmental Microbiology*	97	104
2	Olivier et al. (1999)	*Journal of Chemical Ecology*	80	96
3	Troncoso et al. (2005)	*Food Research International*	79	89
4	Mari et al. (2008)	*Postharvest Biology and Technology*	61	69
5	Velasco et al. (2013)	*Molecules*	40	48
6	Wang et al. (2020)	*RSC Advances*	24	26
7	Eugui et al. (2023)	*Industrial Crops and Products*	16	18
8	Kara and Soylu (2020)	*Journal of Phytopathology*	16	18
9	Troncoso-Rojas et al. (2009)	*Phytoparasitica*	15	16
10	Dagnas et al. (2015)	*International Journal of Food Microbiology*	15	15

Table 4
Works on GSLs and GHPs as a strategy to control postharvest diseases of fresh produce, indicating the study methodology used, the effects and the mechanisms of action involved.

PATHOGEN	DISEASE	GSLs/GHPs ORIGIN	STUDY METHODOLOGY	POSTHARVEST FRESH PRODUCE	EFFECT	GSLs/GHPs INVOLVED	MECHANISM OF ACTION	REFERENCES
Alternaria alternata	Alternaria rot	*Brassica oleracea* var. *capitata* (cabbage) leaves	*In vitro* *In vivo*	Bell pepper fruits	*In vitro*: Pathogen mycelial growth inhibition *In vivo*: Injury reduction	Allyl-, benzyl-, 2-phenylethyl- and phenyl-ITCs	Unidentified	Troncoso et al. (2005)
	Alternaria rot	Commercial ITCs	*In vivo*	Netted melon fruits	Reduction in disease severity	Allyl-ITC	Unidentified	Troncoso-Rojas et al. (2009)
	Leaf spot	*B. oleracea* var. *italica* (broccoli) flower buds	*In vitro* *In vivo*	Arugula leaves	*In vitro*: Pathogen spores' germination inhibition *In vivo*: Reduction in disease severity	Unidentified	Unidentified	Flores-Córdova et al. (2014)
	Alternaria rot	Commercial ITCs *Armoracia rusticana* (horseradish) roots oil	*In vitro* *In vivo*	Tomato fruits	*In vitro*: Pathogen mycelial growth inhibition *In vivo*: Reduction in disease incidence and severity	Benzyl-, 2-phenylethyl- and allyl-ITC	Unidentified	Ren et al. (2020)
	Black spot	Commercial ITCs	*In vitro* *In vivo*	Pear fruits	*In vitro*: Pathogen mycelial growth and spore germination inhibition *In vivo*: Injury reduction	Benzyl-ITC	Destruction of plasma membrane integrity	Wang et al. (2020)
	Alternaria rot	*B. oleracea* var. *italica* (broccoli) leaves	*In vitro*	Not indicated	Pathogen mycelial growth inhibition	Glucoraphanin, glucobrassicin and neoglucobrassicin	Unidentified	Eugui et al. (2023)
	Alternaria rot	Modified synthetic GHPs	*In vitro*	Tomato fruits	Pathogen mycelial growth inhibition	Chlorinated-ITC	Thickening of cell walls and mitochondrial vacuolization	Wang et al. (2024)
Botrytis cinerea	Gray mold	*Raphanus raphanistrum* (wild radish) stems and fruits	*In vitro*	Not indicated	Pathogen mycelial growth inhibition	Unidentified	Unidentified	Sánchez-León et al. (2015)
	Gray mold	Commercial ITCs *Armoracia rusticana* (horseradish) roots oil	*In vitro* *In vivo*	Tomato fruits	*In vitro*: Pathogen mycelial growth inhibition *In vivo*: Reduction in disease incidence and severity	Benzyl-, 2-phenylethyl- and allyl-ITC	Unidentified	Ren et al. (2020)
	Gray mold	*B. oleracea* var. *italica* (broccoli) leaves	*In vivo*	Cherry tomato fruits	Injury reduction	Unidentified	Unidentified	Damas-Job et al. (2023)
	Gray mold	*B. oleracea* var. *italica* (broccoli) leaves	*In vitro*	Not indicated	Pathogen mycelial growth inhibition	Glucoraphanin, glucobrassicin and neoglucobrassicin	Unidentified	Eugui et al. (2023)
	Gray mold	*B. oleracea* var. *italica* (broccoli) flower buds, leaves and stems	*In vitro*	Not indicated	Pathogen mycelial growth and spore	Iberin, 3-indoleacetonitrile, 3-butenyl-ITC, indole-3-carboxaldehyde, 5-	Inhibition of fungal defense enzymes	Román et al. (2024)

(continued on next page)

Table 4 (*continued*)

PATHOGEN	DISEASE	GSLs/GHPs ORIGIN	STUDY METHODOLOGY	POSTHARVEST FRESH PRODUCE	EFFECT	GSLs/GHPs INVOLVED	MECHANISM OF ACTION	REFERENCES
					germination inhibition	(methylsulfinyl) pentanenitrile, and 4-(methylsulfinyl) butanenitrile		
	Gray mold	Modified synthetic GHPs	*In vitro*	Tomato fruits	Pathogen mycelial growth inhibition	Chlorinated-ITC	Thickening of cell walls and mitochondrial vacuolization	Wang et al. (2024)
	Gray mold	*B. oleracea* var. *italica* (broccoli) leaves	*In vivo*	Cherry tomato fruits Apple fruits	Reduction in disease severity and incidence	Glucoraphanin, glucobrassicin and neoglucobrassicin	Unidentified	Eugui et al. (2025)
	Gray mold	*B. juncea* (mustard) seeds	*In vitro* *In vivo*	Spinach leaves	*In vitro*: Pathogen mycelial growth inhibition *In vivo*: Injury reduction	Unidentified	Unidentified	Kowalska et al. (2025)
Colletotrichum acutatum	Anthracnose	*R. raphanistrum* (wild radish) stems and fruits	*In vitro*	Not indicated	Pathogen mycelial growth inhibition	Unidentified	Unidentified	Sánchez-León et al. (2015)
	Anthracnose	*B. oleracea* var. *italica* (broccoli) leaves	*In vitro*	Not indicated	Pathogen mycelial growth inhibition	Glucoraphanin, glucobrassicin and neoglucobrassicin	Unidentified	Eugui et al. (2023)
C. gloeosporioides	Anthracnose	*B. oleracea* var. *italica* (broccoli) flower buds	*In vitro*	Mango fruits	Pathogen spores' germination inhibition	Glucoraphanin	Unidentified	Lara-Viveros et al. (2014)
Geotrichum candidum	Sour rot	Commercial ITCs *Armoracia rusticana* (horseradish) roots oil	*In vitro* *In vivo*	Tomato fruits	*In vitro*: Pathogen mycelial growth inhibition *In vivo*: Reduction in disease incidence and severity	Benzyl-, 2-phenyl-ethyl- and allyl-ITC	Unidentified	Ren et al. (2020)
G. citri-aurantii	Sour rot	Commercial ITCs	*In vitro* *In vivo*	Mandarin fruits	*In vitro*: Pathogen mycelial growth and spore germination inhibition *In vivo*: Injury reduction	Benzyl-, methyl-, allyl-and ethyl-ITC	Unidentified	Kara and Soylu (2020)
Helminthosporium solani	Silver scurf	*Brassica nigra* (black mustard) and *B. juncea* (Indian mustard) leaves	*In vitro*	Potato tubers	Pathogen mycelial growth inhibition	Allyl-ITC	Unidentified	Olivier et al. (1999)
Monilinia fructicola	Brown rot	*Brassica napus* subsp. *napus* (canola) and *B. juncea* (Indian mustard) stems, leaves and flowers	*In vitro* *In vivo*	Peach fruits	*In vitro*: Pathogen mycelial growth and spore germination inhibition *In vivo*: Injury reduction	Unidentified	Unidentified	Pazolini et al. (2016)
	Brown rot	*Rapistrum rugosum* (bastard cabbage) stems, leaves and flowers and *Tropaeolum majus* (nasturtium) stems and leaves	*In vitro*	Stone fruits	Pathogen mycelial growth inhibition	Unidentified	Unidentified	Stegmayer et al. (2022)

(*continued on next page*)

Table 4 (*continued*)

PATHOGEN	DISEASE	GSLs/GHPs ORIGIN	STUDY METHODOLOGY	POSTHARVEST FRESH PRODUCE	EFFECT	GSLs/GHPs INVOLVED	MECHANISM OF ACTION	REFERENCES
M. laxa	Brown rot	Commercial GHPs *Brassica carinata* (Ethiopian mustard) and *Brassica rapa* (turnip) meals	*In vitro* *In vivo*	Nectarine fruits Peach fruits	*In vitro*: Pathogen mycelial growth and spore germination inhibition *In vivo*: Reduction in disease severity	Allyl- and butenyl-ITC	Unidentified	Mari et al. (2008)
Penicillium corylophilum	No specific name	*B. oleracea* var. *capitata* f. *rubra* (red cabbage) seeds	*In vitro*	Not indicated	Pathogen spores' germination inhibition	Unidentified	Unidentified	Dagnas et al. (2015)
P. expansum	Blue mold	*B. oleracea* var. *italica* (broccoli) leaves	*In vitro*	Not indicated	Pathogen mycelial growth inhibition	Glucoraphanin, glucobrassicin and neoglucobrassicin	Unidentified	Eugui et al. (2023)
P. digitatum	Green mold	*B. napus* subsp. *napus* (canola) and *B. juncea* (Indian mustard) stems, leaves and flowers	*In vitro* *In vivo*	Orange fruits	*In vitro*: Pathogen mycelial growth and spore germination inhibition *In vivo*: Injury reduction	Unidentified	Unidentified	Koltz et al. (2020)
Pythium spiculum	Cottony leak	*B. carinata* (Ethiopian mustard) sprouts	*In vitro*	Cucurbits fruits	Pathogen mycelial growth inhibition	Sinigrin, gluconapin, and glucotropaeolin	Unidentified	Arroyo-Cordero et al. (2019)
Rhizopus stolonifer	Soft rot	Commercial ITCs Horseradish (*Armoracia rusticana*) roots oil	*In vitro* *In vivo*	Tomato fruits	*In vitro*: Pathogen mycelial growth inhibition *In vivo*: Reduction in disease incidence and severity	Benzyl-, 2-phenyl-ethyl- and allyl-ITC	Unidentified	Ren et al. (2020)
Sclerotinia sclerotiorum	Sclerotinia rot	Commercial GSLs and ITCs *B. rapa* (turnip) leaves *B. oleracea* (kale, cabbage, tronchuda, broccoli and cauliflower) leaves *B. napus* (nabicol) leaves	*In vitro*	Carrot tuberous roots	Pathogen mycelial growth inhibition	Gluconasturtiin and phenetyl-ITC	Unidentified	Sotelo et al. (2015)
Xanthomonas campestris pv. *campestris*	Black rot	Commercial GSLs and ITCs *B. rapa* (turnip) leaves	*In vitro*	Potato tubers Carrot tuberous roots	Inhibition of pathogenic bacteria proliferation	Gluconapin and gluconapin-ITC	Unidentified	Velasco et al. (2013)
	Black rot	Commercial GSLs and ITCs *B. rapa* (turnip) leaves *B. oleracea* (kale, cabbage, tronchuda, broccoli and cauliflower) leaves *B. napus* (nabicol) leaves	*In vitro*	Potato tubers Carrot tuberous roots	Inhibition of pathogenic bacteria proliferation	Glucobrassicanapin, sinigrin and allyl-ITC	Unidentified	Sotelo et al. (2015)
	Black rot	*B. oleracea* var. *italica* (broccoli) flower buds	*In vitro*	Potato tubers Carrot tuberous roots	Inhibition of pathogenic bacteria proliferation	Sulforaphane	Destruction of plasma membrane integrity	He et al. (2024)

ITC: isothiocyanate.

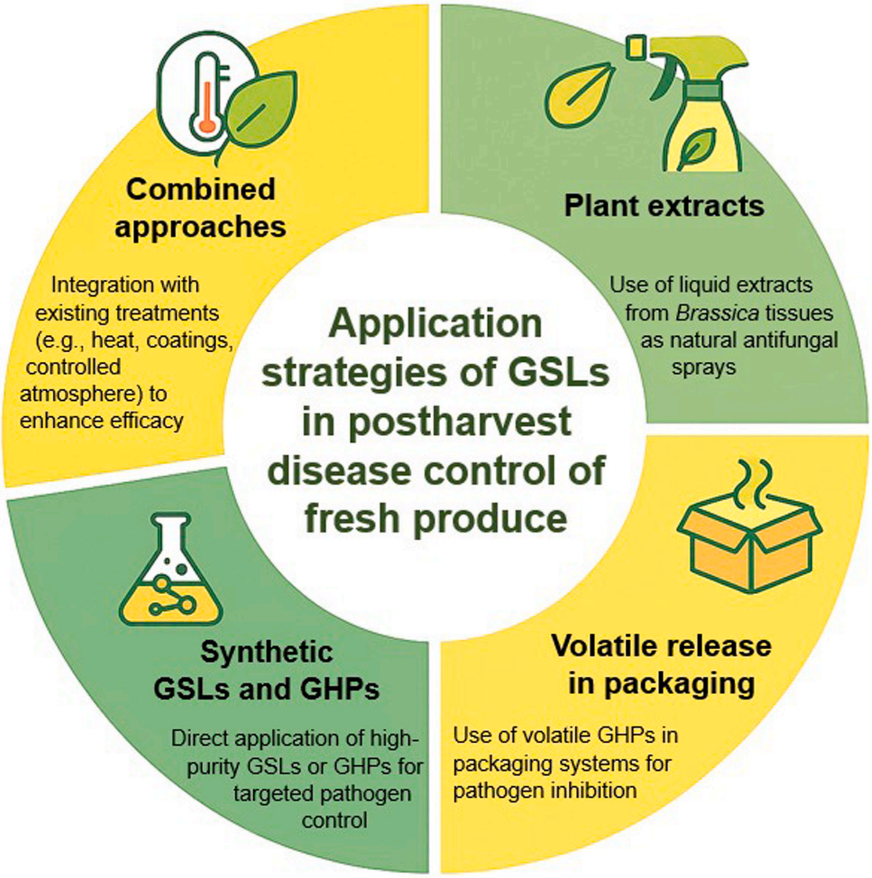

Fig. 2. Summary infographic showing the application strategies of GSLs in controlling different postharvest diseases in non-Brassicaceae fruits and vegetables.

among the top 10 most cited articles, published in the journal *Industrial Crops and Products* in 2023 (Eugui et al., 2023), with 18 (Scopus) and 16 (WoS) citations (Table 3).

To our knowledge, this is the first systematic review to comprehensively analyze the use of GSLs and GHPs in the control of postharvest diseases in non-Brassicaceae fruits and vegetables. This review provides a critical comparison of existing studies and a practical perspective on the applications of these products in the agri-food industry, laying the foundation for future research and their potential implementation in a sustainable agri-food system.

6. GSL and GHP for controlling postharvest diseases in non-brassicaceae fruits and vegetables

The use of GSLs and GHPs in agricultural disease control has been widely studied, especially through biofumigation (discussed in section 4). However, the use of these plant metabolites in postharvest disease control is still in its early stages of development, with only 24 articles published to date. In this review, we have analyzed and discussed all of these studies, which are compiled and classified in Table 4. In addition, the infographic in Fig. 2 provides a graphical summary of the strategies of GSLs use in postharvest disease control of fruits and vegetables.

6.1. *Use of tissues and extracts rich in unidentified GSLs and/or GHPs*

Several studies have successfully inhibited the growth and development of postharvest pathogens *in vitro* using extracts or tissues rich in GSLs, but without identifying the exact metabolites involved in these effects. Ethanol extracts with effective antifungal activity (inhibition of mycelial growth) against postharvest pathogens causing anthracnose (*C. acutatum*) and gray mold (*B. cinerea*) were obtained from stems and fruits of wild radish (*Raphanus raphanistrum*) (Sánchez-León et al., 2015). Also, with hexane and methanol (non-acetone) extracts of bastard cabbage (*Rapistrum rugosum*) and nasturtium (*Tropaeolum majus*) stems, leaves, and flowers against the stone fruit pathogen *Monilinia fruticola* (Stegmayer et al., 2022). Other effects reported *in vitro* include inhibition of conidial germination. The use of aqueous extracts (at 60 °C) of red cabbage (*B. oleracea* var. *capitata* f. *rubra*) seeds significantly inhibited conidial germination of the pathogen *Penicillium corylophilum* (Dagnas et al., 2015). Therefore, different extracts from tissues rich in GSLs and/or GHPs, obtained using very different solvents (water, ethanol, hexane or methanol), can be very effective in controlling postharvest diseases.

These *in vitro* effects have also been confirmed *in vivo*. Mustard seeds (*B. juncea*) inhibited the growth of *B. cinerea in vitro*. When these seeds were placed in atmospheric contact (only the volatiles) with spinach leaves infected with the pathogen, the lesions produced were significantly reduced. In addition, these spinach leaves maintained their sensory and storage characteristics after being treated with the volatiles emitted by the mustard seeds (Kowalska et al., 2025). Therefore, the use of seeds from plants that produce GSLs and GHPs may be an effective industrial strategy for controlling postharvest diseases in different types of packaging.

Other *in vitro* effects reported with GSLs and/or GHPs on postharvest pathogens include the inhibition of conidial germination. With aqueous extracts of broccoli flower buds (*B. oleracea* var. *italica*), the conidial germination of the pathogen *A. alternata* was completely inhibited. Furthermore, when arugula leaves were infected with this pathogen, the severity of the disease was zero with only 2.98 μg/ml of the extracts (Flores-Córdova et al., 2014). Therefore, these extracts rich in GSLs and/or GHPs have high antifungal power, even in low concentrations, and can be totally effective in controlling postharvest diseases. Similarly, aqueous extracts from canola (*B. napus* subsp. *napus*) and Indian mustard (*B. juncea*) leaves and flowers were reported to inhibit *in vitro* conidial germination and mycelial growth of the pathogens *M. fructicola* (Pazolini et al., 2016) and *Penicillium digitatum* (Koltz et al., 2020). These extracts also effectively inhibited the formation of lesions caused by the pathogen in peach and orange fruits, respectively. Furthermore, when treatment with the extracts was combined with other postharvest treatments, such as heat treatment at 50 °C for 30 s, disease inhibition was almost total on peach fruits (Pazolini et al., 2016), not in orange fruits (Koltz et al., 2020). Therefore, combining extracts rich in GSLs and/or GHPs with other postharvest treatments could have additive effects on the control of postharvest diseases, but this needs to be studied on a case-by-case basis.

6.2. Use of strategies with identified GSLs and/or GHPs

In addition to reporting postharvest disease control effects with extracts and tissues rich in GSLs and/or GHPs, these secondary metabolites have also been specifically identified. In a study published in 2019, aqueous extracts were obtained from black mustard (*Brassica nigra*), Chinese mustard (*B. juncea*), Ethiopian mustard (*B. carinata*), and white mustard (*Sinapis alba*) sprouts, and their anti-oomycete activity was studied. Of these extracts, those obtained from Ethiopian mustard were the most effective in inhibiting the *in vitro* growth of the pathogen *P. spiculum*, the causal agent of cottony leak disease in cucurbit fruits. These extracts mainly contained the GSLs sinigrin, gluconapin, and glucotropaeolin, with the first two GSLs also present in the other brassica extracts with lower anti-oomycete effects (Arroyo-Cordero et al., 2019). Therefore, the presence of the GSL glucotropaeolin could imply a higher biocidal capacity of Ethiopian mustard extracts. In addition, white mustard extracts had no anti-oomycete effect and were mainly composed of the GSL sinalbine (Arroyo-Cordero et al., 2019). Similarly, methanolic extracts from turnip (*B. rapa*), kale, cabbage, tronchuda, broccoli, cauliflower (*B. oleracea*) and nabicol (*B. napus*) leaves were effective in inhibiting the *in vitro* growth of postharvest pathogens of potato tubers and carrot tuberous roots. Specifically, against the bacterium *X. campestris* pv. *campestris*, the causal agent of black rot, and the fungus *S. sclerotiorum*, the causal agent of sclerotinia rot. The GSLs present in these brassica leaf extracts that are possibly involved in their antimicrobial effect are gluconasturtiin and gluconapin (Velasco et al., 2013; Sotelo et al., 2015). Therefore, the antimicrobial effect of GSL-rich tissue extracts depends specifically on the profile of these compounds. In this regard, specific GSLs have been isolated from extracts and used individually. Against the pathogen causing mango anthracnose (*C. gloeosporioides*), the GSL glucoraphanin isolated from broccoli flower bud extracts was used *in vitro*. This specific GSL completely inhibited the conidial germination of *C. gloeosporioides* (Lara-Viveros et al., 2014).

The choice of starting material for obtaining extracts rich in GSLs and/or GHPs, as well as their storage method, can be key factors in their antimicrobial activity and in the profile of bioactive compounds obtained. A study published in 2023 proposed the use of harvest residues from broccoli plantations, specifically their leaves, to obtain extracts rich in GSLs with biopesticidal capacity. It was determined that leaves obtained from organic crops had a higher GSL content than those obtained from conventional crops (using agrochemicals). In addition, it was found that freeze-drying the leaves or storing them at −20 or −80 °C had no effect on the GSL profile of the methanolic extracts obtained (Eugui et al., 2023). These extracts were high in the GSLs glucoraphanin, glucobrassicin, and neoglucobrassicin, and were effective in inhibiting the *in vitro* growth of postharvest pathogens that cause black rot (*A. alternata*), gray mold (*B. cinerea*), anthracnose (*C. acutatum*) and blue mold (*P. expansum*). The addition of the enzyme myrosinase to these extracts significantly increased their antifungal capacity (Eugui et al., 2023). Therefore, both GSLs and GHPs exhibit biocidal activity in extracts obtained from brassica tissues, and the addition of exogenous myrosinase enzyme may be essential for its effectiveness. These *in vitro* results were confirmed *in vivo* in cherry tomatoes and apples, but not in table grapes. The extracts were directly effective in controlling gray mold in apples, but when the enzyme myrosinase was also added, they significantly reduced the disease also in cherry tomatoes (Eugui et al., 2025).

Both in tissues and in extracts rich in GSLs, hydrolysis of these metabolites to GHPs can occur, many of which are volatile. In one study, the volatiles emitted by black mustard and Indian mustard leaves macerated by gas chromatography were quantified. In addition, these volatiles were brought into contact with the fungus that causes silver scurf in potato tubers (*Helminthosporium solani*) growing *in vitro*. Specifically, the volatile GHP allyl-ITC was mainly released by these plant tissues and was effective in inhibiting the growth of the pathogen (Olivier et al., 1999). Therefore, brassica tissues could be used in packaging for the natural release of antimicrobial compounds that protect fruits and vegetables in postharvest.

Other GHPs have been described as effective in controlling postharvest diseases, both *in vitro* and *in vivo*. Allyl- and butenyl-ITC GHPs were released from Ethiopian mustard (*B. carinata*) and turnip meals. These GHPs were effective in inhibiting the growth and conidial germination of *Monilinia laxa in vitro*, as well as reducing the severity of brown rot disease in nectarine and peach fruits (Mari et al., 2008). Similarly, oils obtained from horseradish (*Armoracia rusticana*) roots mainly released the volatiles 2-phenylethyl- and allyl-ITC. These GHPs were effective in inhibiting *in vitro* and reducing the incidence and severity of diseases caused by the pathogens *A. alternata* (black rot), *B. cinerea* (gray mold), *Geotrichum candidum* (sour rot) and *Rhizopus stolonifer* (soft rot) in green tomato fruits (Ren et al., 2020).

A further step involves not only identifying the GHP involved in the antimicrobial effect, but also its specific extraction and individual or combined use. Allyl-, benzyl-, 2-phenylethyl- and phenyl-ITCs were identified and extracted from cabbage leaves (*B. oleracea* var. *capitata*). These ITCs were mixed in equal proportions and applied against the pathogen *A. alternata*. *In vitro*, the mixture of ITCs completely inhibited the growth of the pathogen at very low concentrations (0.03 mg/ml) (Troncoso et al., 2005). *In vivo*, a study was conducted with bell pepper fruits combining the application of these ITCs with low-density polyethylene bags. This combination of strategies resulted in less lesion formation than with the commercial fungicide control treatment. In addition, all fruit quality parameters were maintained, such as general appearance, fresh weight loss, and firmness (Troncoso et al., 2005). Therefore, the combination of GHPs with other strategies, such as specific packaging, can promote greater protective capacity against postharvest diseases and the possibility of industrial development of the methodologies.

To date, few mechanisms of action have been identified in GSLs and GHPs for the control of postharvest diseases in non-Brassicaceae fruits and vegetables. Sulforaphane is a GHP present in different tissues of *Brassica* species, including broccoli flower buds. In 2024, it was described how sulforaphane inhibited the proliferation of the postharvest pathogenic bacterium *X. campestris* in potato tubers and carrot tuberous roots by destroying its plasma membrane integrity (He et al., 2024). The GHPs iberin, 3-indoleacetonitrile, 3-butenyl-ITC, indole-3-carboxaldehyde, 5-(methylsulfinyl) pentanenitrile, and 4-(methylsulfinyl) butanenitrile were also identified and isolated from broccoli tissues, specifically from flower buds, leaves, and stems. An *in vitro* study determined that these GHPs inhibited both mycelial growth and conidial germination of the pathogen *B. cinerea*. Subsequently, an *in* *silico* study determined how these GHPs acted against the fungus by inhibiting its defense enzymes eburicol 14-alpha-demethylase and glutathione-S-transferase (Román et al., 2024). Therefore, GHPs can act against different cellular and molecular structures of postharvest pathogens, and further research in this area is essential.

6.3. Use of strategies with commercial or synthesized GSLs and/or GHPs

Today, GSLs and GHPs can be purchased commercially, without having to extract them from plant tissues (Abdelshafeek and El-Shamy, 2023). Several *in vitro* studies have determined that both GSLs and their GHPs, both commercial, are effective in inhibiting different postharvest pathogens. Specifically, gluconapin and gluconapin-ITC, and gluconasturtiin and phenetyl-ITC were effective against the pathogenic fungus *S. sclerotiorum* and the pathogenic bacterium *X. campestris* (Velasco et al., 2013; Sotelo et al., 2015).

Most studies conducted with commercial products have been carried out with GHPs, determining their *in vitro* capacity to inhibit pathogens and subsequently *in vivo* to control the disease they cause in postharvest. The GHPs studied with antifungal efficacy have been allyl-ITC (Mari et al., 2008; Troncoso-Rojas et al., 2009; Kara and Soylu, 2020; Ren et al., 2020), benzyl-ITC (Kara and Soylu, 2020; Ren et al., 2020), 2-phenylethyl-ITC (Ren et al., 2020), methyl-ITC (Kara and Soylu, 2020), ethyl-ITC (Kara and Soylu, 2020) and butenyl-ITC (Mari et al., 2008). These GHPs have been effective in controlling diseases caused by the pathogens *A. alternata* (Troncoso-Rojas et al., 2009; Ren et al., 2020), *B. cinerea* (Ren et al., 2020), *Geotrichum citri-aurantii* (Kara and Soylu, 2020), *G. candidum* (Ren et al., 2020), *R. stolonifer* (Ren et al., 2020) and *M. laxa* (Mari et al., 2008), on netted melon (Troncoso-Rojas et al., 2009), tomato (Ren et al., 2020), mandarin (Kara and Soylu, 2020), nectarine and peach (Mari et al., 2008) fruits. Therefore, commercially available GHPs may be an effective industrial application alternative for controlling different postharvest diseases in different fruits and vegetables.

The mechanisms of action involved in the antimicrobial effectiveness of these commercial GHPs have been identified to a very limited extent. In a study conducted in 2020, propidium iodide staining, relative electrical conductivity, and lysis ability assays were used to analyze the mode of action of a commercial benzyl-ITC on the pathogen *A. alternata* (Wang et al., 2020). This GHP was able to inhibit *in vitro* the mycelial growth and conidial germination of the pathogen, as well as the black spots formed on pear fruits. Specifically, this antifungal activity was due to direct destruction of the integrity of the fungal plasma membrane (Wang et al., 2020). Further work is needed to identify the mechanisms of action developed by these commercial products.

Another line of research with GHPs for use in post-harvest disease control is based on their chemical modification to increase their antimicrobial activity. In a recently published study (2024), chlorinated ITCs were used effectively in the *in vitro* inhibition of the postharvest pathogens *A. alternata* and *B. cinerea*. The mode of action of this new modified compound was determined in *B. cinerea*, describing its ability to cause thickening of cell walls and mitochondrial vacuolization (Wang et al., 2024). Therefore, the targeted modification of GHPs can increase the biocidal capacity of these compounds in their postharvest use, increasing the diversity of possible mechanisms of action involved.

7. Conclusions

Postharvest diseases in fruits and vegetables are a major cause of losses in the agri-food industry. Environmental and health problems associated with the use of chemical pesticides, together with legislative bans on their use, are driving the search for new alternatives that are sustainable and effective. In this context, the use of biocidal plant extracts and compounds may be an effective alternative for the present and future, where GSLs and GHPs may represent an important source for the development of new marketable products for widespread use.

8. Future prospects

Several studies have reported the efficacy of plant tissue extracts rich in GSLs and GHPs in controlling postharvest diseases, even at very low concentrations. In addition, the use of different solvents (water, ethanol, hexane, or methanol) allows different profiles of GSLs and GHPs to be extracted, all of which are effective as postharvest biocides. These results exemplify the great antimicrobial power of these secondary plant metabolites. In this sense, not only do extracts have an effective biocidal effect against postharvest diseases, but specific isolated metabolites are equally effective. Future work should focus on establishing industrially scalable systems for extracting these biocidal metabolites from different plant tissues in the most effective and sustainable way possible. In addition to developing marketable formulations and products, adjusting effective and safe application doses, and finding ways to maintain their shelf life for as long as possible.

Although many different plant extracts and tissues have shown effectiveness in controlling postharvest diseases, exhaustive analysis of the profiles of GSLs and GHPs present has shown that this effect is highly dependent on the plant species from which they are isolated and their secondary metabolite profile. In addition, depending on the form of cultivation, significant differences have also been reported, with plants grown organically accumulating the highest levels of GSLs in their tissues. Therefore, it is necessary to carry out mass metabolomics research with different plant species and tissues rich in GSLs, as well as different cultivation systems, to determine which could be the best raw material for obtaining the best product for postharvest use.

When studying strategies based on GSLs and reporting different efficiencies in their use as biocides, one must always ask oneself and, as far as possible, confirm whether it is these metabolites that are responsible for the results obtained or their GHPs. In this regard, antimicrobial effects have been determined in postharvest, specifically for both GSLs and GHPs. However, the addition of the enzyme myrosinase to GSL-rich extracts increased their protective capacity against different diseases. Therefore, future work should always attempt to elucidate whether the effectiveness of an extract or tissue as a postharvest biocide is due to one metabolite or another. In addition, research should be conducted on the exogenous application of myrosinase in extracts or tissues for postharvest use, studying not only its effectiveness but also its cost and possible industrial application.

In addition to the use of GSLs and GHPs specifically isolated from plant extracts, these compounds have also been used very effectively in their commercial form. For their actual use in the agri-food industry, studies should be carried out on their large-scale application and effectiveness, as well as a study of their economic profitability, as they are high-purity and costly compounds. Related to this, studies have also been conducted on how targeted chemical modification of these metabolites significantly increases their antimicrobial capacity. This area of study is still very underdeveloped and represents a significant knowledge gap that requires significant research efforts at both the basic and applied levels.

Following the exhaustive analysis carried out in this review, it has been found that there is a significant knowledge gap regarding the mechanisms of action that both GSLs and GHPs develop against postharvest pathogens. It is important to carry out future work to determine not only the efficacy of specific tissues, extracts, and metabolites as protectors against these diseases, but also to deepen our understanding of what happens at the cellular and molecular level and why. Developing truly efficient and sustainable strategies requires knowledge of how they work and what effects their use has.

The application methods for all the strategies included in this review are very diverse. For example, it has been determined that the use of seeds and other plant organs (such as leaves) rich in GSLs gradually releases GHPs in volatile form with great efficacy in controlling postharvest diseases. This strategy should be developed to a commercial level through different strategies, such as including these plant tissues in

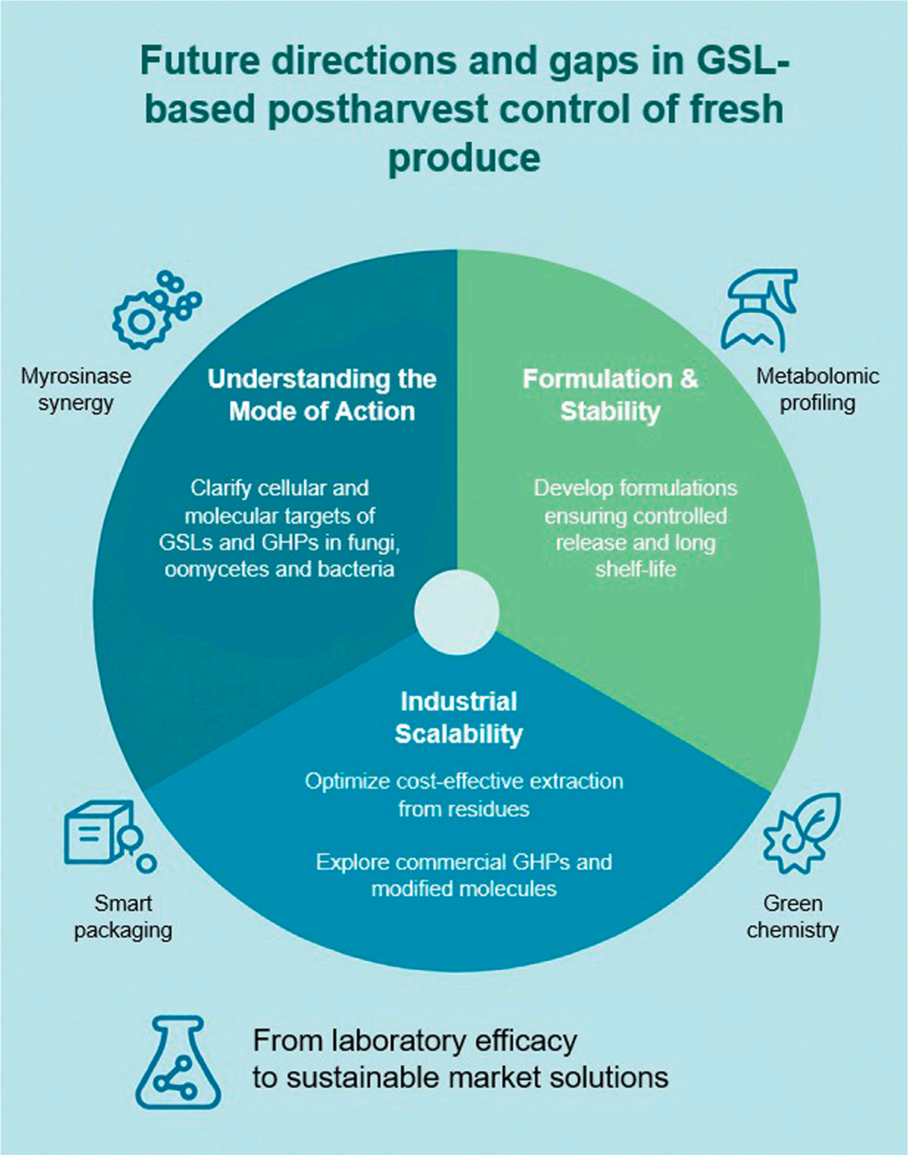

Fig. 3. Summary infographic showing future directions and gaps in GSL-based postharvest control of non-Brassicaceae fruits and vegetables.

fruit and vegetable packaging.

Finally, several studies have been conducted combining the use of GSLs and GHPs in postharvest protection with other strategies already used in the agri-food industry. For example, when combined with thermotherapy, inhibitions of these diseases of up to 100 % have been reported. Or with the use of specific packaging, such as low-density polyethylene bags, synergistic effects have been reported in the protection of fresh products. Therefore, future work should study these combinations of strategies in depth, along with their efficiency and possible industrial applicability, in search of more sustainable postharvest management. The infographic in Fig. 3 provides a graphical summary of the future challenges and gaps in GSL-based postharvest control in non-Brassicaceae fruits and vegetables.

CRediT authorship contribution statement

Daniel Eugui: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation. **Pablo Velasco:** Writing – review & editing. **Jorge Poveda:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

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

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