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Biological control of postharvest diseases in pome fruits using endophytic microorganisms: Innovative sustainable strategies for greater food security

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A B S T R A C T

Postharvest diseases cause significant losses in pome fruit production (5–50%), and growing pathogen resistance to synthetic fungicides demands sustainable alternatives. Endophytic microorganisms offer promising biological control, employing diverse antagonistic mechanisms. A systematic literature review of 25 peer-reviewed articles (1996–2025) identified key bacterial genera (*Bacillus*, *Pseudomonas*, *Pantoea*) and fungal endophytes (*Aureobasidium*, *Metschnikowia*) as effective biocontrol agents. These microorganisms achieve 50–85% disease reduction through nutrient competition, antimicrobial metabolite secretion (lipopeptides), and host immune system activation—performance comparable to commercial biocontrol products. However, critical research gaps persist in formulation optimization, scalability validation, industry-standard protocol integration, and expanded host species coverage (pears, kiwifruit). Developing robust delivery systems remains an essential priority. Endophytic microorganisms represent a sustainable approach to reduce chemical inputs while enhancing food security and supply chain resilience.

1. Introduction

The ongoing growth of the global population, estimated to approach 8.2 billion by 2030 and about 10 billion by 2050, places considerable pressures on food security and sustainable agriculture (Becker and Fanzo, 2023). Simultaneously, United Nations agencies emphasize that progress in reducing hunger has stalled, with approximately 673 million people (≈ 8.2% of the global population) experiencing undernourishment in 2024 (FAO, 2025). This combination of demographic pressure and persistent food insecurity demands a substantial expansion of food production systems under challenging ecological, social and regulatory constraints.

Projections indicate that global food supply must increase by approximately 50–70% by 2050 relative to early 21st-century levels, as outlined in seminal Food and Agriculture Organization (FAO) assessments, while subsequent meta-analyses have refined these estimates to 35–56% (FAO, 2009; van Dijk et al., 2021). However, meeting this projected demand sustainably is challenged by the slowing rate of yield gains, limited land availability, climate change, water scarcity, and ongoing ecosystem degradation.

Moreover, substantial fractions of agricultural output are lost postharvest, particularly among highly perishable horticultural commodities such as fruits and vegetables. FAO and associated reports estimate that about 14% of food is lost between harvest and retail globally, with losses higher for fresh produce. Postharvest loss rates for fruits and vegetables are variably cited in the literature, often ranging from 28% to 55%, depending on region, infrastructure and handling practices (Karoney et al., 2024; Kumari et al., 2022). Such losses represent a substantial inefficiency in the food system and heighten the imperative for improved postharvest disease control.

A major contributor to postharvest losses is disease, most notably fungal decay during handling, storage and transport. These losses translate into economic losses amounting to billions of dollars annually and exacerbate global food insecurity (Wenneker and Thomma, 2020; Droby et al., 2025). Among pome fruits, key postharvest pathogens include *Penicillium expansum* (blue mold), *Botrytis cinerea* (gray mold), *Alternaria* spp. (black rot) and *Colletotrichum* spp. (bitter rot). Depending on cultivar susceptibility, storage conditions, and pathogen pressure, losses in pome fruit systems may range from 5% to 50% (Cozzolino et al., 2020; Wenneker and Thomma, 2020).

Traditional postharvest disease control has relied heavily on synthetic fungicides, which, despite their proven efficacy, raise concerns

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regarding environmental contamination, human health risks, and the emergence of resistant pathogen strains (Wenneker and Thomma, 2020; Yin et al., 2023). Moreover, increasing regulatory restrictions and consumer demand for residue-free produce are further constraining the continued use of chemical fungicides (Kumari et al., 2022). In this context, the growing emphasis on sustainable agriculture and integrated pest management (IPM) has positioned biological control as a central component of modern strategies aimed at reducing chemical dependence (Droby et al., 2025). Consistent with this trend, global market forecasts indicate a rapid expansion of biopesticide technologies, with the sector projected to grow from USD 8.73 billion in 2024 to USD 28.62 billion by 2032 (Fortune Business Insights, 2025). Among biological approaches, the use of beneficial microorganisms—particularly endophytic species—has gained traction as a sustainable alternative for postharvest disease mitigation (Droby et al., 2025). Endophytes are especially promising due to their capacity for internal colonization, intimate host association, and diverse antagonistic mechanisms (Huang et al., 2020; Morales-Cedeño et al., 2021). Because they reside within plant tissues, these microorganisms are often less vulnerable to environmental fluctuations and may exhibit greater persistence under commercial postharvest conditions.

This review aims to provide a comprehensive and up-to-date analysis of endophytic microorganisms as postharvest biocontrol agents in pome fruits. Specifically, it seeks to (1) assess the agricultural and economic significance of pome fruits, (2) analyze principal postharvest pathogens and current control strategies, (3) summarize the mechanisms and application potential of endophytic biocontrol agents, and (4) identify research gaps and propose future directions for sustainable integration of endophytic biocontrol in postharvest systems.

2. Pome fruits: agricultural and economic importance and postharvest processing

Pome fruits, including apples, pears, quinces, and other members of the Rosaceae family, represent one of the most economically significant fruit categories worldwide (Musacchi et al., 2021; Sousa et al., 2022). They contribute substantially to international trade, support food security, and play a key role in rural economies across both developed and developing regions.

Apple production dominates the global pome fruit market, with worldwide production reaching approximately 84 million tons in the 2024/25 season. China leads global apple production with 48 million tons (57% of global production), followed by the European Union with 11.01 million tons (13% of global production). Other significant producers include the United States, Turkey and India (FAO, 2024). Pear production represents the second-largest segment with global production forecast at 25.9 million tons in 2024/25, with China dominating at 20.2 million tons (78% of global production) and the European Union contributing 1.9 million tons (FAO, 2024).

The economic value of pome fruit industries is substantial. In South Africa, the combined turnover for pome and stone fruit sectors reached ZAR 19.7 billion (approximately USD 1.1 billion) in the 2023/24 marketing year (Cloete and Davids, 2024). Pome fruits constitute a significant portion of international agricultural trade, with approximately 45% of total production destined for export markets. Export volumes have shown positive trends, with apple exports reaching 48.42 million cartons (12.5 kg each) in 2024, representing an 11% increase compared to the previous season, and pear exports totaling 20.06 million cartosn (12.5 kg each), showing an 8% year-on-year increase (Steenkamp, 2024). In Europe, organic pome fruit production has shown notable growth, with Italy leading at 9000 ha producing over 200,000 tons, followed by Poland (5500 ha, 117,600 tons), Hungary (3810 ha, 10.78% annual growth), and Spain (2520 ha, 9.56% annual growth) in 2023 (Willer et al., 2025).

The global fresh fruit supply chain faces unique challenges due to long supply lead times combined with significant supply and demand uncertainties, making pome fruits particularly vulnerable to postharvest losses and quality degradation during transportation and storage phases (Wu et al., 2019; Kumari and Dhingra, 2024).

2.1. *Postharvest processing and supply chain management*

Postharvest processing of pome fruits consists of a coordinated series of operations intended to preserve quality, maximize shelf life, and ensure safety across the supply chain. The postharvest phase begins immediately after harvest and includes critical stages such as precooling, cleaning, sorting, packaging, storage, and transportation, each presenting opportunities for quality maintenance but also risks for pathogen contamination and disease development (Pace and Cefola, 2023; Rodrigues et al., 2024).

Modern postharvest facilities employ sophisticated technologies to optimize fruit quality and minimize losses. Cold storage systems maintain optimal temperatures and humidity levels, with controlled atmosphere storage being particularly important for apples to slow respiration rates and reduce decay incidence (Wu et al., 2019; Rodrigues et al., 2024). The application of postharvest treatments, including 1-methylcyclopropene (SmartFresh), has become increasingly common in commercial operations to extend storage life and maintain fruit quality (Win et al., 2021; Yoo et al., 2021). Quality assessment and sorting technologies have evolved significantly, with modern facilities utilizing deep learning and computer vision systems to evaluate quality traits and detect defects, enabling precise sorting based on multiple quality parameters and reducing disease spread risk during storage (Pathmanaban et al., 2023; Zhong et al., 2023). Advanced packaging technologies, including modified atmosphere packaging and active packaging systems, help maintain optimal storage conditions and reduce pathogen development (Kumari and Dhingra, 2024; Ogurlu et al., 2024).

Despite technological advances, postharvest management of pome fruits faces several critical challenges. Temperature management throughout the cold chain remains a primary concern, as temperature fluctuations can accelerate ripening, increase respiration rates, and promote pathogen development, requiring significant infrastructure investments and operational expertise (Wu et al., 2019; Rodrigues et al., 2024). Pathogen contamination represents a major risk occurring at multiple points including field harvest, transportation, processing facilities and storage environments, where organic matter, inadequate sanitation and suboptimal storage conditions promote pathogen proliferation and disease incidence (Cozzolino et al., 2020; Amiri et al., 2024). Water quality management is essential, as insufficiently treated or recycled water can introduce microbial hazards, making adherence to strict safety standards, regular water quality monitoring, and effective sanitization protocols recognized as best practices (FDA, 2018; Kumari and Dhingra, 2024). The increasing complexity of global supply chains, with extended transportation times and varying storage conditions across different regions, compromises fruit quality and increases disease risks, while climate change impacts add further complexity to postharvest logistics and storage management (Larue and Ker, 2024; Rojas-Reyes et al., 2024).

3. Postharvest diseases in pome fruits: losses caused and control strategies

The most economically important postharvest diseases of pome fruits are caused by a relatively small number of fungal pathogens with worldwide distribution. *Penicillium expansum*, the causal agent of blue mold, stands as the most destructive postharvest pathogen affecting apples and pears globally, typically infecting fruits through wounds, lenticels and bruises, causing characteristic blue-green sporulation and soft, watery rot that spreads rapidly through stored fruit lots (Luciano-Rosario et al., 2020; Wang et al., 2021).

Botrytis cinerea, causing gray mold, represents the second most important postharvest pathogen of pome fruits. This ubiquitous fungus can infect fruits at any stage from bloom to postharvest, remaining latent during fruit development and becoming active under storage conditions, with infections originating from calyx-end infections during bloom or stem-end damage during harvest and handling operations (Romanazzi et al., 2016). *Alternaria* species, particularly *A. alternata*, cause significant postharvest losses through infections that typically occur through skin breaks, sunburn, bruising, or physiological disorders, characterized by dark, sunken lesions that expand rapidly under favorable storage conditions (KC and Rasmussen, 2020; DeShields and KC, 2021). Other significant postharvest pathogens include *Cladosporium herbarum*, *Colletotrichum* species causing bitter rot and *Neofabraea* species responsible for bull's-eye rot (Wenneker et al., 2020; Amiri et al., 2024). The complex nature of postharvest disease development often involves multiple pathogens acting synergistically to accelerate fruit deterioration.

Postharvest diseases contribute substantially to economic losses in the global pome fruit supply chain. In well-resourced production systems, disease-related losses typically account for 5–25% of harvested apples and pears by volume; in less-developed or poorly managed supply chains, losses reach up to 50% before fruit reaches consumers (FAO, 2019; Argenta et al., 2021; Shewa et al., 2022). Given that annual global pome fruit production exceeds 100 million tonnes, such losses correspond to billions of dollars in economic damage each year. Under optimal controlled-atmosphere storage conditions with proper temperature and humidity control, decay losses typically remain below 10%, whereas poor temperature or humidity management and high pathogen pressure can result in losses exceeding 25% (Konstantinou et al., 2011; Argenta et al., 2021).

The economic impact of postharvest diseases extends beyond direct fruit losses to encompass costs for sorting, repackaging and downgrading of quality, which reduce market value. Infected fruit also functions as a reservoir of inoculum, promoting secondary infections during storage and distribution. Furthermore, mycotoxin contamination—particularly patulin produced by *P. expansum*—imposes additional costs for food-safety monitoring and compliance with regulatory limits (≤50 μg/kg in many jurisdictions) (Zhong et al., 2018; Bacha et al., 2023).

3.1. Control strategies

Traditional postharvest disease management in pome fruits depends primarily on synthetic chemical fungicides applied as postharvest dips, in edible coatings, or integrated into packaging. The principal fungicide classes—benzimidazoles (e.g., thiabendazole), demethylation inhibitors (DMIs, e.g., imazalil) and strobilurins (e.g., pyraclostrobin)—target microtubule formation, ergosterol biosynthesis and mitochondrial respiration, respectively, displaying application- and dose-dependent efficacy against key storage pathogens (Chakraborty et al., 2024; Szczygieł et al., 2024).

However, their effectiveness is increasingly inconsistent due to rapid development of pathogen resistance. Multiple resistance profiles to thiabendazole, pyrimethanil and fludioxonil have been documented in *P. expansum* isolates from apple storage, while *B. cinerea* populations have evolved resistance to succinate dehydrogenase inhibitors (SDHIs), with H272R and H272Y mutations in the SdhB subunit being reported across diverse hosts (Alzohairy et al., 2023; Zhou et al., 2024a; Puglisi and Amiri, 2025). Concurrently, regulatory agencies have progressively restricted or withdrawn several postharvest fungicides, narrowing the repertoire of approved chemistries for disease control (European Commission, 2024).

Consumer preference for pesticide-free and organic produce intensifies market pressure to reduce synthetic inputs, with pesticide-free labels typically commanding price premiums of 38.3–93.7% above conventional products (Nitzko et al., 2024). Environmental sustainability imperatives and occupational health concerns—including documented risks of respiratory diseases, neurological disorders and acute health effects among packing-house workers—are driving greater adoption of biological and physical disease control methods (Tessema et al., 2022; Onwudiegwu et al., 2025).

Physical approaches—such as controlled-atmosphere storage, modified-atmosphere packaging and precise temperature management—are essential to integrated postharvest disease management. However, when deployed alone under commercial conditions with high pathogen pressure or imperfect environmental control, these methods often fail to fully suppress decay, necessitating integration with additional biological or chemical interventions (Fang and Wakisaka, 2021). Heat treatments such as hot water dips and vapor heat treatments have demonstrated efficacy against surface-dwelling pathogens but pose challenges in maintaining fruit quality and scaling for commercial operations (Palumbo et al., 2022). Ultraviolet-C (UV-C) radiation offers promising reductions in decay but requires precise calibration of dose and exposure time to avoid adverse effects on sensory and nutritional attributes (Esua et al., 2019; Sonntag et al., 2023).

Integrated pest management (IPM) strategies combine multiple control approaches—cultural practices, physical treatments, reduced-risk chemical applications and biological control agents—in coordinated programs designed to minimize disease losses while addressing sustainability concerns (Guan et al., 2023; Zhou et al., 2024b). Sanitation practices involving thorough cleaning and disinfection of harvest containers, processing equipment and storage facilities lower pathogen inoculum reservoirs, with novel methods including UV-C irradiation and generally recognized as safe (GRAS) substances effectively reducing fungal viability (Luciano-Rosario et al., 2025). Maintaining a consistent cold chain (0–4 °C) inhibits pathogen proliferation during storage and transport, while harvest timing, handling practices and pre-harvest fungicide applications—when properly timed within two weeks before harvest—provide residual protection during early storage phases (Prange and Wright, 2023; Horska et al., 2025).

Biological control agents (BCAs) have become essential to IPM programs as sustainable alternatives to synthetic fungicides, offering effective pathogen suppression via competition for space and nutrients, production of antimicrobial metabolites, induction of host defense responses including plant-defense hormonal activation (Poveda, 2020), and physical niche exclusion. BCAs such as *Bacillus amyloliquefaciens*, *Pseudomonas fluorescens* and antagonistic yeasts (e.g., *Wickerhamomyces anomalus*) have demonstrated efficacy in reducing postharvest decay in pome fruits under commercial conditions. Endophytic fungi represent an additional category of BCAs with particular promise in postharvest disease management (Díaz-Urbano et al., 2023), offering complementary mechanisms of action and enhanced persistence within plant tissues. Multiple studies document decay reduction rates ranging from 50 to 85% depending on the specific strain, pathogen and environmental conditions (Fenta et al., 2023; Droby et al., 2025; Lawal et al., 2025). Beyond conventional biological control agents, emerging alternative strategies leverage plant secondary metabolites for postharvest disease suppression. Glucosinolates and their hydrolysis products derived from *Brassica* species have demonstrated efficacy as sustainable control agents against postharvest diseases in non-Brassicaceae fruits and vegetables (Eugui et al., 2026). These bioactive compounds can be efficiently extracted from broccoli biomass—a widely available agricultural by-product—and integrated into postharvest protocols (Eugui et al., 2025), offering a circular-economy approach that valorizes plant residues while reducing reliance on synthetic fungicides. By deploying multiple modes of action, BCAs mitigate the risk of resistance development and reduce chemical inputs, aligning with regulatory and consumer demands for residue-free produce.

Climate change poses significant challenges for postharvest disease management, with shifts in temperature and humidity altering pathogen life cycles and virulence, leading to increased disease pressure and changing storage requirements. The globalization of food supply chains has created new pathways for pathogen dissemination, demanding enhanced surveillance systems and adaptive management strategies incorporating real-time monitoring and risk-based interventions

(Youssef et al., 2023; AESAN Scientific Committee, 2025). Technological advances in pathogen detection and monitoring offer substantial improvements through early-warning systems and predictive analytics, with high-throughput molecular diagnostics and sensor networks enabling rapid identification of latent infections. Integration of digital technologies—such as Internet-of-Things (IoT) sensor arrays for real-time tracking of temperature, humidity and volatile organic compounds—facilitates precision application of control measures, optimizing fungicide dosing and biological agent deployment to enhance efficacy and reduce inputs (Wang et al., 2024; Rhouma, 2025). The development of pathogen resistance to biological control agents, while less documented than fungicide resistance, represents a potential future challenge requiring resistance management strategies including the rotation of BCAs and use of multi-strain formulations to maintain long-term control efficacy (Fenta et al., 2023; Droby et al., 2025).

4. Endophytic microorganisms as BCAs against postharvest diseases

Endophytic microorganisms represent a remarkable biological resource with immense potential for sustainable management of postharvest diseases. They inhabit the internal tissues of plants—including stems, leaves, roots, fruits and seeds—spending all or part of their life cycles within host tissues without causing visible symptoms or damage. This lifestyle contrasts with epiphytes, which inhabit plant surfaces and pathogens, which provoke disease symptoms. These beneficial microorganisms establish complex symbiotic relationships that have evolved over millions of years, with the endophytic niche representing a sophisticated ecological adaptation whereby microbes and plants engage in mutualistic or commensal relationships, enhancing host fitness through nutrient exchange, stress mitigation and defense against biotic and abiotic challenges (Hardoim et al., 2015; Fagorzi and Mengoni, 2022; Gupta and Saxena, 2023).

The diversity of endophytic microorganisms is extraordinary, with virtually all plant species studied harboring diverse bacterial and fungal taxa. The colonization patterns vary significantly among microbial species and plant tissues, with some endophytes exhibiting high host specificity while others possess broader host ranges. Environmental factors—including geographic location, climate conditions and plant physiological status—profoundly shape endophytic community composition and diversity (Fagorzi and Mengoni, 2022; Anand et al., 2023).

The ecological relationships between endophytes and their plant hosts represent complex biological partnerships that have coevolved over evolutionary time scales. Plants provide endophytes with nutrients, protection from environmental stress and stable ecological niches, while endophytes contribute to plant health through growth promotion, stress tolerance enhancement and pathogen resistance (Tiwari and Bae, 2020; Fagorzi and Mengoni, 2022; Anand et al., 2023). These symbiotic relationships extend beyond simple nutritional exchanges to include complex biochemical communications and metabolic interactions, with some endophytes acquiring the ability to produce bioactive compounds identical to those synthesized by their host plants, suggesting horizontal gene transfer events during coevolutionary processes (Tiwari and Bae, 2020; Fagorzi and Mengoni, 2022; Anand et al., 2023).

4.1. *Biocontrol potential and advantages*

Endophytic microorganisms employ diverse mechanisms to suppress plant pathogens and enhance plant health, often operating synergistically to provide robust and durable protection (Fadiji and Babalola, 2020). These mechanisms include competition for space and nutrients, production of antimicrobial metabolites, direct antagonism through lytic enzymes, induction of host defense responses and enhancement of plant vigor through growth promotion activities.

However, while defense induction is well-documented in pre-harvest contexts, its role in postharvest fruit—characterized by mature, non-growing tissues—requires more critical evaluation. The temporal feasibility of eliciting effective defenses during storage remains constrained, and observed biochemical changes (e.g., enzyme activity, phenolic accumulation) are frequently correlated with reduced decay but not yet unequivocally demonstrated as the primary causal mechanism of disease suppression (Prusky and Romanazzi, 2023; Prusky et al., 2025).

Endophytic microorganisms offer several distinct advantages over other biological control approaches for postharvest disease management. Their internal colonization of plant tissues provides protection from environmental stresses and harsh conditions that often limit the effectiveness of externally applied BCAs (Mengistu, 2020; Ling et al., 2024). The co-evolutionary relationships between endophytes and their hosts have led to a mutual "balanced antagonism," whereby endophytes are naturally adapted to the host environment and do not trigger strong defense responses or phytotoxic effects (Khare et al., 2018; Pathak et al., 2022). The diverse mechanisms of action employed by endophytes provide robust protection against pathogen resistance development by targeting multiple pathways simultaneously, contrasting with chemical fungicides with single-site modes of action that can rapidly select for resistant pathogen strains (Fadiji and Babalola, 2020).

Importantly, while strains reviewed here were originally isolated as endophytes from healthy plant tissues, most postharvest applications involve surface application to harvested fruits rather than relying on pre-harvest internal colonization. Thus, 'endophytic origin' primarily serves as a strain discovery source rather than reflecting true postharvest endophytism, distinguishing these BCAs from purely epiphytic applications while leveraging endophyte-associated traits like multi-mechanism antagonism.

4.2. *Current research status and future challenges*

Research on endophytic microorganisms as BCAs has expanded rapidly, driven by increasing recognition of their potential applications and the urgent need for sustainable pest management solutions. Advances in molecular biology and omics technologies have revolutionized endophyte research, enabling detailed characterization of endophytic communities and identification of bioactive metabolites through next-generation sequencing and metabolomics approaches (Chen et al., 2022; Mishra et al., 2022). Recent advances in microencapsulation, fermentation technologies and delivery systems have demonstrated promising potential to enhance shelf life, controlled release and stability under field conditions (Ganeshan et al., 2021; Arias-Chavarría et al., 2024).

Despite significant promise, commercial development of endophytic biocontrol agents faces key challenges. Host specificity remains a major issue, with highly specific strains delivering strong pathogen suppression but limited broad applicability, while endophytes capable of colonizing multiple hosts often demonstrate lower efficacy against particular pathogens. Regulatory approval requires extensive safety assessments and efficacy trials, making the process costly and time-consuming (Helepciuc and Todor, 2022; Saberi-Riseh et al., 2021). Scaling up production and ensuring quality control present substantial hurdles, as large-scale fermentation must maintain consistent cell viability and biological activity while downstream formulation processes guarantee long shelf life and stability (Ganeshan et al., 2021; Saberi-Riseh et al., 2021). Successful incorporation into existing postharvest management systems demands careful alignment with conventional treatments and precise timing of application. This integration requires the development of management protocols that define compatible combinations with chemical or physical treatments, optimal intervention schedules and suitable storage parameters.

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 "(endophyte OR endophytic fungi OR endophytic bacteria) AND (pome fruits OR pipefruits OR apple OR pear OR quince OR medlar OR kiwifruit OR nashi) AND (post-harvest OR postharvest) disease". 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", 46 results were retrieved (search performed on October 6, 2025). Of these 46 articles, 25 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", 71 results were retrieved in Scopus (search performed on October 6, 2025), of which 22 were not related to the subject of this work, therefore, 24 articles were included in the review. For the initial inclusion and exclusion of all articles obtained in the search, a thorough reading of the following sections was carried out: Title, Abstract, Keywords, Results, Discussion and Conclusions. The classification of articles as "not related to the subject" refers to documents whose topics of study do not coincide with the use of endophytic microorganisms for the control of postharvest diseases in pomefruits. It is important to note the overlapping results between the two databases. Of the 21 articles used from WoS and the 24 from Scopus, 20 coincide, contributing 1 and 4 unique articles, respectively. Therefore, the total number of final articles of the review on the use of endophytic microorganisms for the control of postharvest diseases in pomefruits was 25 articles.

The first article on this topic was published in 1996 (Mari et al., 1996). However, no further publications were made until 2004 (with 2 articles). Between 2004 and 2019, the average number of publications per year was 2 articles, with a maximum of 4 articles (in 2010) and years without publications (2006, 2008, 2011–2013, 2015, 2018, and 2019). Between 2020 and 2025, a total of 10 articles have been published, with a maximum in 2020 (five articles) and no publications in 2024 (Fig. 1a).

In terms of the authors' countries of affiliation, China was the country with the most articles, with 6. It was followed by Italy, with 4 articles,

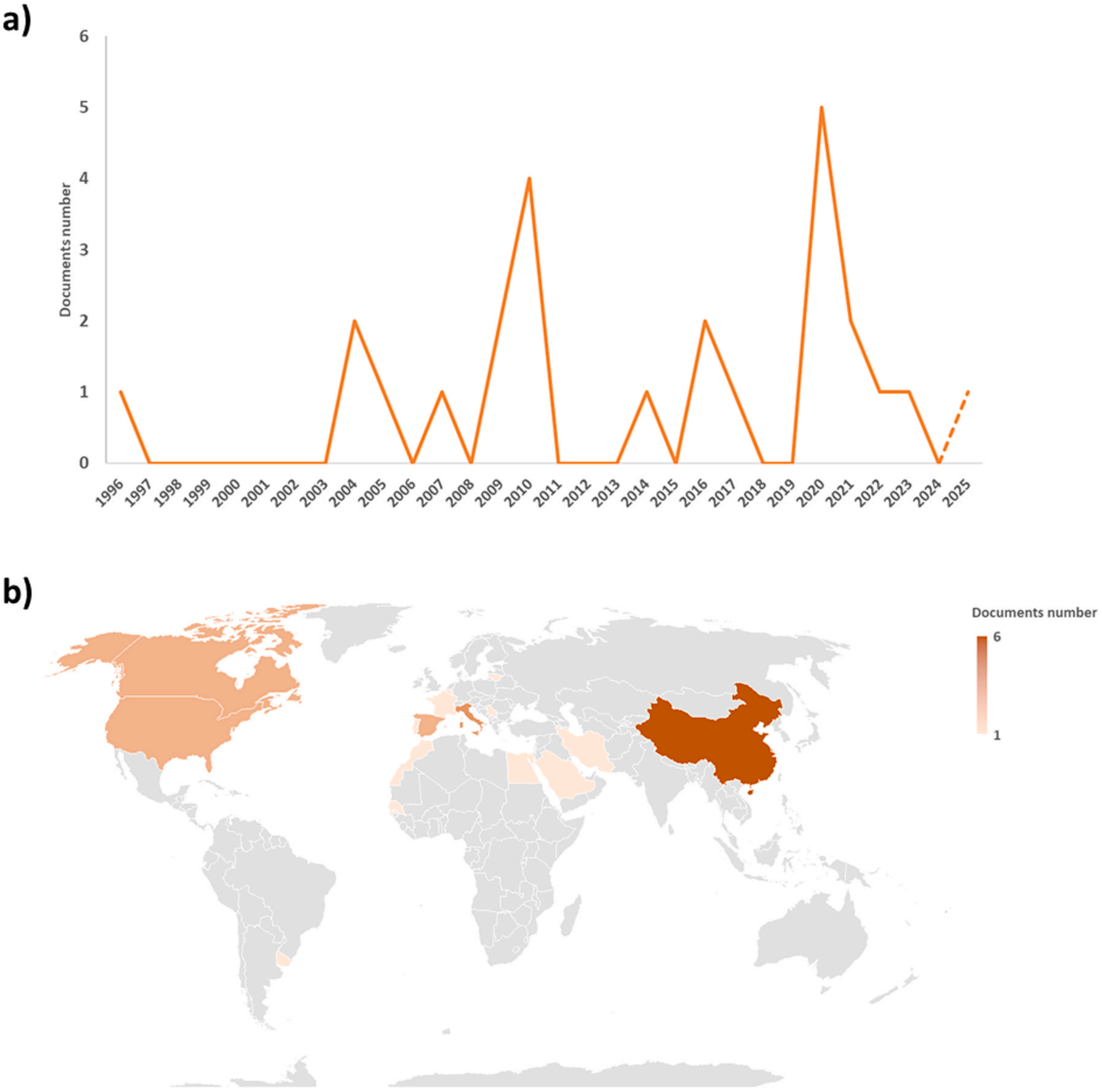

Fig. 1. Graphical representation of the data obtained in the bibliographic search. Number of articles per year (a) and countries of authors (b), the legend represents the number of articles per country. As only articles published in the year 2025 up to the month of October have been analyzed, this year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

Canada, the USA, and Spain, with 3 articles, and Korea, with 2 articles. With one publication, we found a total of 12 countries from Asia (Iran, Saudi Arabia and Turkey), Africa (Egypt, Morocco and Senegal), America (Uruguay), and Europe (Belgium, France, Lithuania, Portugal and Serbia) (Fig. 1b).

These authors published their articles in 18 different journals, including *Biological Control* and *Postharvest Biology and Technology* (with 4 articles), and Journal of Applied Microbiology (with 2 articles). The other journals published 2 or 1 article (Table 1). In terms of the number of citations received by these articles, the one published in the *Journal of Applied Microbiology* in 2004 (Touré et al., 2004) stands out, with 278 (Scopus) and 259 (WoS). In second and third place are two articles published in the journal *Postharvest Biology and Technology* (Mercier and Jiménez, 2004; Calvo et al., 2020), with 202 and 180 citations in Scopus, respectively, and 172 and 166 citations in WoS, respectively. None of the ten most cited articles are less than five years old (Table 2).

6. Endophytic microorganisms as BCAs against postharvest diseases of pome fruits

As explained above, endophytic microorganisms can represent an effective and sustainable strategy for controlling diseases that cause postharvest losses. The following section describes and analyzes the different studies conducted on the use of endophytic microorganisms as BCAs against postharvest diseases in pome fruits. Table 3 compiles all the work carried out to date on this topic, indicating the reported effects and mechanisms of action involved. In addition, Fig. 2 is an infographic summary showing the different endophytic microorganisms used as BCAs against postharvest diseases in different pomefruits, indicating the main effects and mechanisms of action described.

Table 1
Journals where the reviewed papers were published.

JOURNAL	NUMBER OF PAPERS	PAPERS REFERENCES
Biological Control	4	Mari et al., 1996; Zhang et al., 2010; Madbouly et al., 2020; Fernandez-San Millan et al., 2021
Postharvest Biology and Technology	4	Mercier and Jiménez, 2004; Chen et al., 2016; Wallace et al., 2017; Calvo et al., 2020
Journal of Applied Microbiology	2	Touré et al., 2004; Lee et al., 2009
Biocontrol Science and Technology	1	Vero et al., 2009
Canadian Journal of Microbiology	1	Spadaro et al., 2010
Food Microbiology	1	Li et al., 2025
Horticulturae	1	Yang et al., 2023
International Journal of Food Microbiology	1	Banani et al., 2014
Journal of Applied Sciences Research	1	Ramin et al., 2007
Journal of Food Biochemistry	1	Pang et al., 2020
Journal of Horticultural Science & Biotechnology	1	Torres et al., 2005
Microbial Pathogenesis	1	Lahlali et al., 2020
Microorganisms	1	Pan et al., 2022
Phytopathology	1	Bian et al., 2021
The Plant Pathology Journal	1	Park et al., 2010
World Journal of Microbiology and Biotechnology	1	Manso et al., 2010
Yeast	1	Agirman and Erten, 2020
Zemdirbyste-Agriculture	1	Miliute et al., 2016

Table 2
Number of citations of the 10 most cited articles.

RANKING	REFERENCE	JOURNAL	WoS CITATIONS	Scopus CITATIONS
1	Touré et al., 2004	*Journal of Applied Microbiology*	259	278
2	Mercier and Jiménez, 2004	*Postharvest Biology and Technology*	172	202
3	Calvo et al., 2020	*Postharvest Biology and Technology*	166	180
4	Zhang et al., 2010	*Biological Control*	103	114
5	Mari et al., 1996	*Biological Control*	94	112
6	Wallace et al., 2017	*Postharvest Biology and Technology*	71	86
7	Spadaro et al., 2010	*Canadian Journal of Microbiology*	71	83
8	Agirman and Erten, 2020	*Yeast*	66	70
9	Fernandez-San Millan et al., 2021	*Biological Control*	62	75
10	Madbouly et al., 2020	*Biological Control*	59	66

6.1. Endophytic microorganisms BCAs against postharvest diseases in apple fruits

Several studies have been conducted in recent decades using endophytic bacteria as BCAs against postharvest pathogens in apples. In the vast majority of these studies, the mechanisms of action involved in microbial biocontrol capacity have been identified. However, there are bacteria whose mechanisms of action are still unknown. A strain of *Pantoea ananatis*, an endophyte isolated from the skin of orange fruit, was effective in reducing the incidence of blue mold (*P. expansum*) in postharvest apple fruits. Although this bacterium reduced the disease by up to 85%, the mechanisms of action involved are unknown (Manso et al., 2010). Therefore, it is necessary to investigate the possible mechanisms of action involved in these postharvest biocontrol capabilities.

To control blue mold in apples, different strains of endophytic bacteria isolated from pulse crop roots have been used, all of them belonging to the *Pseudomonas fluorescens* species. When applied to fruit by immersion in a bacterial suspension, a significant reduction in decay incidence and lesion diameter was achieved after 15 weeks of storage at 1 °C. This biocontrol effect could be due, among other mechanisms, to the parasitic capacity of these bacteria on the conidia and hyphae of *P. expansum*. This mechanism was confirmed by observing bacterial adhesion to the pathogen and reporting the release of protease lytic enzymes (Wallace et al., 2017). Other endophytic bacteria also reported this parasitic capacity in the protection of apple fruits; specifically, *Alcaligenes faecalis* and *Pantoea agglomerans*, isolated from stigmas of quince blossoms. Applying these bacteria to wounds in apple fruits significantly reduced the disease severity caused by the pathogens *Monilinia fructigena* and *M. laxa*. Among the mechanisms of action involved, the production of lytic enzymes, such as proteases, was confirmed. In addition, the efficiency of controlling postharvest disease with the use of these bacteria was similar to that of other commercially used bacterial products and slightly lower than that of a commercial chemical fungicide (thiophanate-methyl) (Lahlali et al., 2020). Therefore, bacterial parasitism on fungal pathogens is an effective mechanism of action in apple postharvest, mainly involving the release of protease-type lytic enzymes.

Table 3
Studies conducted on the use of endophytic microorganisms as BCAs against postharvest diseases in pomefruits, indicating the reported effects and mechanisms of action involved.

ENDOPHYTIC ORGANISM			ISOLATED FROM	USED AGAINST (POSTHARVEST PATHOGEN)	FRUITS AND APPLICATION METHOD	EFFECTS	MECHANISMS OF ACTION	REFERENCES
GROUP	SPECIE	STRAIN						
Bacteria	*Alcaligenes faecalis*	ACBC1	Stigmas of quince blossoms	Fungi: *Monilinia fructigena* and *M. laxa*	Apples: 50 μL of 10^8 CFU/mL, directly on wounds	Lower disease severity	Antibiosis by diffusible and volatile antifungal compounds Production and release of lytic enzymes	Lahlali et al., 2020
	Bacillus amyloliquefaciens	2TOE	Mesocarp of tomato fruits	Fugus: *Botrytis cinerea*	Pears: 20 μL of 10^8 cells/mL, directly on wounds	Less lesion diameter and number of infected wounds	Unidentified	Mari et al., 1996
		PG12	Mesocarp of apple fruits	Fungus: *Botryosphaeria dothidea*	Kiwifruits: Immersion of the fruit in a suspension of 10^8 CFU/mL	Lower disease incidence	Antibiosis by diffusible antifungal compounds	Chen et al., 2016
		M9	Kiwifruits	Fungus: *B. dothidea*	Apple: Spraying with cell-free culture filtrates	Lower decay rate	Antibiosis by diffusible antifungal compounds	Pang et al., 2020
	B. pumilus	3PPE	Mesocarp of pepper fruits	Fugus: *B. cinerea*	Pears: 20 μL of 10^8 cells/mL, directly on wounds	Less lesion diameter and number of infected wounds	Unidentified	Mari et al., 1996
	B. subtilis	GA1	Mesocarp of strawberry fruits	Fugus: *B. cinerea*	Apples: 50 μL of 2×10^6-10^8 endospores/mL, directly on wounds Apples: 25 μL of lipopeptide enriched extracts, directly on wounds	Lower disease incidence	Antibiosis by diffusible antifungal compounds	Touré et al., 2004
	B. velezensis	BUZ-14	Apple fruits	Fungus: *Penicillium expansum*	Apples: Treated with 0.01–0.1 mL/L headspace of volatile specific compounds	Lower disease incidence	Antibiosis by volatile antifungal compounds	Calvo et al., 2020
		B1	Roots of orchid	Fungus: *B. dothidea*	Pears: 30 μL of 5×10^7 CFU/mL, directly on wounds	Less lesion diameter	Antibiosis by diffusible antifungal compounds	Yang et al., 2023
	Pantoea sp.	D_8 D_10	Buds of apple trees	Fungus: *Venturia inaequalis*	*In vitro* confrontation	Inhibition of pathogen growth	Unidentified	Miliute et al., 2016
	Pantoea agglomerans	ACBP1	Stigmas of pear blossoms	Fungi: *M. fructigena* and *M. laxa*	Apples: 50 μL of 10^8 CFU/mL, directly on wounds	Lower disease severity	Antibiosis by diffusible and volatile antifungal compounds Production and release of lytic enzymes	Lahlali et al., 2020
	P. ananatis	CPA-3	Mesocarp of apple fruits	Fungus: *P. expansum*	Apples: 25 μL of 10^8 CFU/mL, directly on wounds	Less lesion diameter and number of infected wounds	Competition for space	Torres et al., 2005
		PBC-1	Skin of orange fruits	Fungus: *P. expansum*	Apples: 20 μL of 10^8 CFU/mL, directly on wounds	Lower disease incidence	Unidentified	Manso et al., 2010
	Priestia megaterium	PH3	Peanut seeds	Fungus: *P. expansum*	Pears: 50 μL of 10^9 CFU/mL, directly on wounds	Lower disease incidence	Antibiosis by diffusible antifungal compounds Competition for space Induction of plant defenses	Li et al., 2025
	Pseudomonas fluorescens	D_7	Buds of apple trees	Fungus: *V. inaequalis*	*In vitro* confrontation	Inhibition of pathogen growth	Unidentified	Miliute et al., 2016
		1–112 2–28 4–6	Pulse crops roots	Fungus: *P. expansum*	Apples: Immersion of the fruit in a suspension of 10^8 CFU/mL	Lower disease incidence and less lesion diameter	Competition for space Antibiosis by diffusible and	Wallace et al., 2017

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Table 3 (*continued*)

ENDOPHYTIC ORGANISM			ISOLATED FROM	USED AGAINST (POSTHARVEST PATHOGEN)	FRUITS AND APPLICATION METHOD	EFFECTS	MECHANISMS OF ACTION	REFERENCES
GROUP	SPECIE	STRAIN						
							volatile antifungal compounds Production and release of lytic enzymes	
Fungi	*Aureobasidium pullulans*	ApB	Skin of apple fruits	Fungi: *B. cinerea* and *P. expansum*	Apples: 10 µL of 10^7 CFU/mL, directly on wounds	Lower disease incidence	Competition for nutrients	Vero et al., 2009
		PL5	Plum fruits	Fungi: *B. cinerea* and *P. expansum*	Apples: Immersion of the fruit in a suspension of 10^8 cells/mL	Lower disease incidence	Production and release of lytic enzymes	Zhang et al., 2010
		PL5	Plum fruits	Fungi: *Monilinia fructicola, Alternaria alternata, B. cinerea* and *P. expansum*	Apples: 20 µL of 6.25–62.5 ng/µL of crude lytic enzyme, directly on wounds Apples: expression of the lytic enzyme in *Pichia pastoris* yeast and application 20 µL of 10^8 cells/mL, directly on wounds	Lower disease incidence	Production and release of lytic enzymes	Banani et al., 2014
		GE17	Apple fruits	Fungi: *P. expansum*	*In vitro* confrontation	Inhibition of pathogen growth	Competition for space and nutrients	Agirman and Erten, 2020
	Candida lusitaniae	Cl-28	Grape fruits	Fungus: *P. expansum*	Apples: 5 µL of 10^8 CFU/mL, directly on wounds	Lower disease incidence and severity	Competition for space	Fernandez-San Millan et al., 2021
	C. oleophila	Co-13	Grape fruits	Fungus: *P. expansum*	Apples: 5 µL of 10^8 CFU/mL, directly on wounds	Lower disease incidence and severity	Competition for space	Fernandez-San Millan et al., 2021
	Debaryomyces hansenii	Dh-67	Grape fruits	Fungus: *P. expansum*	Apples: 5 µL of 10^8 CFU/mL, directly on wounds	Lower disease incidence and severity	Competition for space	Fernandez-San Millan et al., 2021
	Epicoccum dendrobii	SMEL1	Branchs of Chinese fir	Fungus: *Colletotrichum gloeosporioides*	Apples: 10 µL of 10^5 spores/mL, directly on wounds	Less lesion diameter	Antibiosis by diffusible antifungal compounds	Bian et al., 2021
	Galactomyces geotrichum	-	Apple fruits	Fungus: *M. fructigena*	Apples: 50 µL of 3 × 10^7 cells/mL, directly on wounds	Lower disease incidence and severity, and less lesion diameter	Production and release of lytic enzymes	Madbouly et al., 2020
	Hypopichia pseudoburtonii	Hp-54	Grape fruits	Fungus: *P. expansum*	Apples: 5 µL of 10^8 CFU/mL, directly on wounds	Lower disease incidence and severity	Competition for space	Fernandez-San Millan et al., 2021
	Metschnikowia pulcherrima	BIO126	Apple fruits	Fungi: *B. cinerea* and *P. expansum*	Apples: Immersion of the fruit in a suspension of 10^7 CFU/mL	Lower disease incidence and severity	Unidentified	Spadaro et al., 2010
	Meyerozyma guilliermondii	37	Source not specified in original study	Fungi: *B. dothidea* and *Diaporthe actinidiae*	Kiwifruits: Immersion of the fruit in a suspension of 10^7 cells/mL	Lower decay rate	Mycoparasitism Competition for space Induction of plant defenses	Pan et al., 2022
	Muscodor albus	620	Cinnamon tree bark	Fungi: *B. cinerea* and *P. expansum*	Apples: Rice grains colonized by the endophyte	Lower disease incidence	Antibiosis by volatile antifungal compounds	Mercier and Jiménez, 2004
		620	Cinnamon tree bark	Fungi: *B. cinerea, P. expansum* and *Sclerotinia sclerotiorum*	Apples: Rye grains colonized by the endophyte	Lower disease incidence	Antibiosis by volatile antifungal compounds	Ramin et al., 2007
	Nodulisporium sp.	CF016	Cinnamon tree stem	Fungi: *B. cinerea* and *P. expansum*	Apples: Wheat bran–rice hull colonized by the endophyte	Less lesion radius	Antibiosis by volatile antifungal compounds	Park et al., 2010
	Oxyporus latemarginatus	EF069	Pepper roots	Fungus: *B. cinerea*	Apples: Wheat bran–rice hull colonized by the endophyte	Lower disease incidence	Antibiosis by volatile antifungal compounds	Lee et al., 2009
	Pichia kudriavzevii	-	Apple fruits	Fungus: *M. fructigena*	Apples: 50 µL of 3 × 10^7 cells/mL, directly on wounds	Lower disease incidence and severity, and less lesion diameter	Production and release of lytic enzymes	Madbouly et al., 2020

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Table 3 (*continued*)

ENDOPHYTIC ORGANISM			ISOLATED FROM	USED AGAINST (POSTHARVEST PATHOGEN)	FRUITS AND APPLICATION METHOD	EFFECTS	MECHANISMS OF ACTION	REFERENCES
GROUP	SPECIE	STRAIN						
	Schwanniomyces vanrijiae	-	Apple fruits	Fungus: *M. fructigena*	Apples: 50 µL of 3×10^7 cells/mL, directly on wounds	Lower disease incidence and severity, and less lesion diameter	Production and release of lytic enzymes	Madbouly et al., 2020

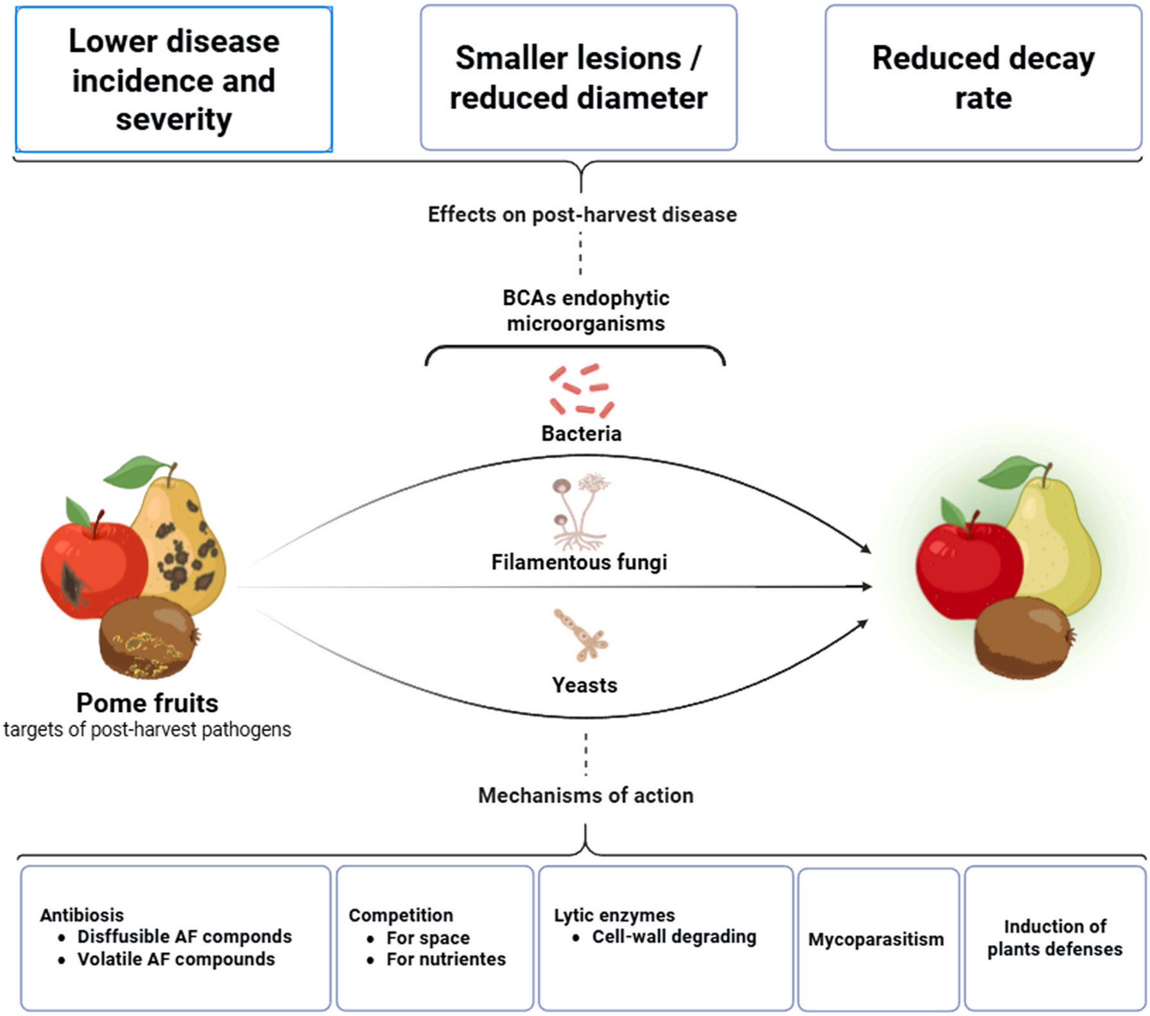

Fig. 2. Summary infographic showing the different endophytic microorganisms used as BCAs against postharvest diseases in different pomefruits, indicating the main effects and mechanisms of action described.

Another mechanism of action identified in endophytic bacteria used to control these postharvest diseases is competition for space. This mechanism of action was also reported in endophytic strains of *P. fluorescens*, isolated from pulse roots, in the control of *P. expansum* in apple fruits. The rapid colonizing capacity of the fruit surface, stored at low temperatures (1 °C), was related to a lower incidence and diameter of lesions in the fruits (Wallace et al., 2017). On the other hand, the strain of *P.a ananatis* CPA-3, an endophyte of apple mesocarp, reduced the diameter and number of lesions infected by blue mold in apple fruits, both in cold storage and at 20 °C. This effect was the result of rapid and massive colonization of the wounds by the bacteria. In addition, the bacteria are unable to grow at the pH and temperatures present in the human stomach, making their presence in consumed fruit safe (Torres et al., 2005). Therefore, competition for space is a mechanism of action developed by endophytic bacteria that is effective in controlling these diseases in apples.

In other endophytic bacterial strains, antibiosis has been identified as their main mechanism of action against postharvest diseases in apple fruits. The most studied group of metabolites in these endophytic bacteria are diffusible metabolites, particularly lipopeptides. Against the pathogen *B. cinerea*, the endophytic bacterium *Bacillus subtilis* (strain GA1) reduced the incidence of disease by up to 80% through direct application to wounds as endospores or as lipopeptide-enriched extracts. Specifically, the metabolites identified in these antifungal extracts belong to lipopeptides of the iturin, fengycin and surfactin families (Touré et al., 2004). Endophytic strains of *Bacillus amyloliquefaciens* also produce diffusible lipopeptides that are effective in controlling postharvest diseases in apples. Specifically, immersing the fruit in bacterial suspensions (strain PG12) reduced the decay rate caused by the pathogen *Botryosphaeria dothidea* by more than 70%. The lipopeptides identified with effective antifungal activity belonged to the iturin and fengycin families, which caused a lumpy appearance and abnormal structure of the pathogen mycelia (Chen et al., 2016). Therefore, the production of diffusible metabolites by endophytic bacteria is an effective mechanism of action in controlling fungal postharvest diseases in apple fruits. However, further research is needed to identify the non-lipopeptide metabolites involved and to develop new strategies for the direct application of these metabolites in industry.

Also within antibiosis, endophytic bacteria can release antimicrobial metabolites in the form of volatile compounds. The bacteria *A. faecalis* and *P. agglomerans* are capable of significantly reducing disease severity caused by the pathogens *M. fructigena* and *M. laxa* by releasing both diffusible and volatile metabolites. However, only diffusible lipopeptides from the bacillomycin, fengycin, iturin and surfactin families were identified (Lahlali et al., 2020). On the other hand, diffusible and volatile metabolites involved in their effectiveness as BCAs in postharvest apples have been identified in different endophytic strains of *P. fluorescens*. Specifically, against the pathogen *P. expansum*, these bacteria were able to significantly reduce disease incidence and lesion diameter through the action of the diffusible metabolite phenazine-1-carboxylic acid and volatile hydrogen cyanide (Wallace et al., 2017). Moreover, there are also endophytic bacteria that can inhibit the development of blue mold in apple fruit solely through the production and release of volatile metabolites. The BUZ-14 strain of *Bacillus velezensis* produces the volatile metabolites benzaldehyde and diacetyl, which, when applied to stored fruit, significantly reduce the incidence of the disease (Calvo et al., 2020). Therefore, the production of volatile metabolites is also an effective mechanism of action in controlling these postharvest diseases. Furthermore, their isolation allows for the development of new application strategies in active packaging during the postharvest commercialization of fruit.

In addition to the work carried out with endophytic bacteria in apples, endophytic fungi have also been studied as effective BCAs against postharvest diseases in apples. In some cases, the mechanisms of action involved have not been identified, although their controlling capacity is evident. For example, the endophytic yeast *Metschnikowia pulcherrima* (strain BIO126) applied to apples by immersion in cell suspension reduced the incidence of the pathogens *B. cinerea* and *P. expansum* by up to 58% and the severity of the diseases by up to 70% (Spadaro et al., 2010).

With regard to parasitism, endophytic fungi have not been reported to attach to postharvest pathogens in apples. However, these fungi produce lytic enzymes related to this mechanism of action and involved in their effectiveness as BCAs. Several apple endophytic yeasts (*Galactomyces geotrichum*, *Pichia kudriavzevii* and *Schwanniomyces vanrijiae*) applied to fruit wounds together with the pathogen *M. fructigena* reduced the incidence of postharvest disease by up to 90%. This biocontrol capacity was a direct result of the production and release by these yeasts of lytic enzymes such as chitinases, pectinases, β-1,3-glucanases and proteases (Madbouly et al., 2020). These same groups of lytic enzymes were reported in the endophytic yeast *Aureobasidium pullulans* (strain PL5), capable of reducing the incidence of the pathogens *B. cinerea* and *P. expansum* in apples by 50% (Zhang et al., 2010). Subsequently, it was identified that the lytic enzyme mainly involved in this control capacity was alkaline serine protease. First, the enzyme was applied directly to wounds on apples infected by the pathogens *Monilinia fructicola*, *A. alternata*, *B. cinerea* and *P. expansum*, confirming its antifungal activity. Subsequently, the enzyme was expressed in the yeast *Pichia pastoris*, confirming that the presence of the enzyme gave the bacteria biocontrol capacity against the indicated pathogens (Banani et al., 2014). Therefore, the production of lytic enzymes by endophytic yeasts is an effective mechanism of action in controlling various postharvest pathogens in apples. However, further research is needed to determine its possible involvement in parasitic activities and how its production is activated.

Competition for space and nutrients has also been reported as an effective mechanism of action in controlling these postharvest diseases caused by endophytic yeasts. The ApB strain of *A. pullulans* significantly reduced the incidence of diseases caused by *B. cinerea* and *P. expansum*. This biocontrol capacity was directly related to the ability of this yeast to produce siderophores and remove iron from the surrounding environment (Vero et al., 2009). Along with their ability to chelate nutrients, endophytic yeasts can compete for space by growing faster than postharvest pathogenic fungi. In this regard, different yeasts isolated from grape fruits (*Candida lusitaniae*, *C. oleophila*, *Debaryomyces hansenii* and *Hypopichia pseudoburtonii*) reduced the incidence and severity of the disease caused by *P. expansum* in apples through the rapid formation of biofilms on wounds (Fernandez-San Millan et al., 2021). Therefore, both competition for space and nutrients are mechanisms of action developed by endophytic yeasts against postharvest pathogens in apples. Future work could delve deeper into the use of different formulations for applying yeasts, which could favor their establishment and growth on the surface of apples.

Endophytic filamentous fungi, but not yeasts, have been described as effective BCAs against postharvest diseases in apples through antibiosis. Mostly, these fungi act by releasing volatile antifungal metabolites. However, *Epiccocum dendrobii* (strain SMEL1), which was isolated from branches of Chinese fir, is capable of producing effective diffusible antifungal metabolites in postharvest. Specifically, using the organic solvent ethyl acetate, metabolites capable of inhibiting the diameter of lesions formed by the pathogen *C. gloeosporoides* in apples are obtained from *E. dendrobii* (Bian et al., 2021). Therefore, the production of diffusible metabolites by endophytic fungi is an effective mechanism for controlling postharvest diseases in apples. However, further work is needed to identify this mechanism in other filamentous fungi and yeasts, as well as to identify these antifungal metabolites.

When the mechanism of action used by these endophytic filamentous fungi is the production of volatile antifungal metabolites, they are applied using cereal grains colonized by the fungi and placed at the bottom of the container holding the apples; this system is called fumigation. The use of rice or rye grains colonized by the endophyte *Muscodor albus* to fumigate apples significantly reduced the disease incidence caused by *B. cinerea*, *P. expansum* and *Sclerotinia sclerotiorum*. The fumigation periods lasted between 24 and 72 h, without affecting the quality of the fruit, such as firmness, soluble solid content, and titratable acidity (Mercier and Jiménez, 2004; Ramin et al., 2007). Similar biocontrol effects were reported in other filamentous fungi colonizing bran–rice hull, such as *Nodulisporium* sp. or *Oxyporus latemarginatus*, through the main release of the volatile antifungal metabolites β-elemene and 5-pentyl-2-furaldehyde, respectively (Lee et al., 2009; Park et al., 2010). Therefore, the production of volatile metabolites by filamentous endophytic fungi is an effective mechanism for controlling these postharvest diseases. Application strategies could be developed using modified atmospheres in packaging.

6.2. *Endophytic microorganisms BCAs against postharvest diseases in pear fruits*

To date, no studies have been conducted on endophytic fungi to manage postharvest diseases in pears, but studies have been conducted on endophytic bacteria. A pioneering study isolated 175 endophytic bacteria from different fruits and vegetables, of which two (*B. amyloliquefaciens*, strain 2TOE, and *B. pumilus*, strain 3PPE) were studied against the pathogen *B. cinerea* in pears. The application of these bacteria to pear wounds reduced the diameter and number of lesions caused by the pathogen. In addition, both bacteria were compatible with chemical fungicide treatments such as iprodione-based ones (Mari et al., 1996). Therefore, endophytic bacteria can be used in combination with chemical fungicides to control postharvest diseases in pears. However, further work is needed to identify the possible mechanisms of action involved.

One of the mechanisms of action reported for these bacteria in pears has been antibiosis through diffusible metabolites. Specifically, *B. velezensis* (strain B1), an orchid root endophyte, is capable of producing a battery of lipopeptides from the surfactin, iturin and fengycin families, which reduce the diameter of lesions caused by the pathogen *B. dothidea* by more than 70% (Yang et al., 2023). Antibiotic action is therefore an effective mechanism developed by endophytic bacteria. However, further research is needed to describe this mechanism of action in other bacterial species and strains, as well as application strategies that directly utilize antifungal metabolites.

Another mechanism of action that has not yet been discussed in these endophytic microorganisms is the induction of plant responses. The endophytic bacterium *Priestia megaterium* (strain PH3), isolated from peanut seeds, is capable of significantly reducing blue mold in pears. This bacterium rapidly and effectively colonizes wounds in fruits and induces a defensive response by their tissues. Specifically, *P. megaterium* causes an increase in the activity of various defensive enzymes (superoxide dismutase, catalase, ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase) and in the local accumulation of phenolic compounds and flavonoids (Li et al., 2025). Therefore, the induction of plant defenses is a mechanism of action developed by these bacteria and effective in controlling postharvest diseases in pears. This mechanism of action should be further studied in other bacterial strains and species, allowing the development of new and effective strategies for managing postharvest diseases.

6.3. *Endophytic microorganisms BCAs against postharvest diseases in other pomefruits*

In addition to apples and pears, to date, work has only been carried out on the control of postharvest diseases in kiwifruits within the pomefruits. Among endophytic bacteria, one was isolated from kiwifruit, called *B. amyloliquefaciens* (strain M9). After applying cell-free culture filtrates of this bacterium to kiwifruit by spray, the decay rate caused by the pathogen *B. dothidea* was reduced by more than 70%. This antifungal effect of the bacterial filtrates was due to the presence of a diffusible metabolite called C12-surfactin A lipopeptide (Pang et al., 2020). Therefore, endophytic bacteria may be an effective strategy for controlling postharvest diseases in kiwifruits through the production of diffusible antifungal metabolites. However, further work is needed with other bacterial strains and species to identify new effective mechanisms of action.

Among endophytic fungi, possible BCAs effective against postharvest diseases of kiwifruit have also been sought. To date, only one endophytic yeast, *Meyerozyma guilliermondi* (strain 37), has been reported as an effective BCA. When applied by immersing the fruit in a cell suspension, this yeast was able to reduce natural decay caused by the pathogens *B. dothidea* and *Diaporthe actinidiae* by more than 30%, while maintaining soft-ripe quality. *M. guilliermondi* acts against these pathogens through different mechanisms of action, which do not include the production of antifungal metabolites. This yeast effectively parasitizes the mycelium of pathogens and grows rapidly on the surface of fruits. In addition, it is capable of inducing a series of defensive responses in plant tissues, including increased enzymatic activity and local accumulation of antioxidant compounds (Pan et al., 2022). Therefore, endophytic yeasts can act as effective BCAs against postharvest diseases in kiwifruits through different mechanisms of action. However, further research is needed to identify new endophytic yeasts and filamentous fungi that can be used in the formulation of effective kiwifruit disease management strategies in the food industry.

7. Conclusions and future prospects

The present review of 25 published articles reveals that endophytic microorganisms represent a promising strategy for controlling postharvest diseases in pome fruits. The research highlights that bacterial genera such as *Bacillus*, *Pseudomonas* and *Pantoea*, alongside endophytic yeasts such as *A. pullulans* and *M. pulcherrima*, exhibit significant antagonistic efficacy through multiple complementary mechanisms—including competition for space and nutrients, production of antimicrobial metabolites (particularly lipopeptides), mycoparasitism via lytic enzyme secretion and induction of host defenses. For instance, endophytic *P. fluorescens* strains controlling *P. expansum* in apples combine the production of the diffusible metabolite phenazine-1-carboxylic acid with volatile hydrogen cyanide, while the kiwifruit yeast *M. guilliermondii* simultaneously exploits nutrient and space competition, mycoparasitism and induction of host defense enzymes, illustrating the synergistic nature of these multi-mechanistic interactions. The convergence of multiple control mechanisms may theoretically reduce resistance risks over single-mode fungicides, pending field validation. Decay reduction rates in controlled trials range from 50 to 85%, depending on the endophytic strain, target pathogen and storage conditions, indicating preliminary efficacy comparable to conventional biological control products.

Across host species, nutrient and space competition and the production of diffusible antifungal metabolites (particularly *Bacillus* lipopeptides) are consistently reported in apples, pears and kiwifruit, whereas induction of host defense responses has been mechanistically characterized in detail only for a few systems, notably Nanguo pear and kiwifruit, suggesting potential host-specific responsiveness. Endophytic yeasts and bacteria in apples most frequently rely on mycoparasitism mediated by lytic enzymes and on the combined action of diffusible and volatile metabolites, while current evidence in pears and kiwifruit is dominated by lipopeptide-mediated antibiosis and defense priming, with parasitism and enzymatic mechanisms still underexplored.

However, the systematic analysis reveals pronounced research gaps that constrain practical commercialization. The literature exhibits marked bias toward apple fruits, with substantial gaps in knowledge regarding endophytic BCAs for pears, quinces and other minor pome fruits. Of the 25 articles reviewed, the vast majority focused on apples, leaving pear, quince and kiwifruit systems severely underrepresented. Additionally, many endophytic strains retain incompletely characterized mechanisms of action; field applications have relied predominantly on basic suspension formulations lacking optimization for commercial shelf-life and stability; and large-scale field trials remain essentially absent from the literature, limiting assessment of real-world performance under diverse storage and distribution conditions.

Future research must prioritize expanding species coverage to encompass pear and other neglected pome fruits, leveraging omics technologies to elucidate molecular mechanisms underlying biocontrol capacity. In particular, metagenomic and metabolomic approaches offer powerful insights into the hidden diversity and functional potential of unculturable endophytes, enabling the discovery of novel biosynthetic gene clusters, antimicrobial metabolites, and signaling molecules. Development of improved formulation and delivery systems—such as microencapsulation, fermentation optimization, and consortial approaches—should also integrate advanced encapsulation technologies, including nanocarriers and bio-based polymeric matrices, to enhance formulation stability, shelf-life, and controlled release of active microbial and metabolic components. Integration of endophytic BCAs with chemical and physical postharvest treatments requires systematic compatibility studies and development of standardized protocols defining optimal intervention timing and parameter ranges. Future work should also evaluate potential synergistic interactions between endophytes and postharvest treatments such as 1-MCP, UV-C irradiation or controlled atmosphere storage, as these combinations may potentiate host defense priming and disable pathogen virulence. Such integration protocols are essential for realizing consistent commercial efficacy within existing postharvest infrastructure.

Broader commercial translation demands multidisciplinary collaboration encompassing microbial production at scale, standardized quality control methodologies, regulatory framework development aligned with current biosafety requirements and rigorous economic feasibility analysis that quantifies benefits beyond direct disease suppression—including reduced chemical dependency, extended shelf-life economics and broader sustainability metrics. Emerging technologies such as precision temperature monitoring, real-time pathogen detection via molecular diagnostics, IoT-enabled supply chain tracking and advanced formulation strategies may further enhance biocontrol outcomes and market viability. The integration of IoT-based environmental and pathogen sensors with endophytic biocontrol systems could enable predictive and adaptive disease management strategies, where data-driven models optimize timing and dosage of microbial applications in response to early infection or stress signals.

Ultimately, successful integration of endophytic BCAs could support loss reduction efforts within commercial settings, decrease reliance on synthetic chemical inputs and contribute meaningfully to global food security and agricultural sustainability objectives through environmentally sound management practices aligned with evolving regulatory and consumer demands.

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CRediT authorship contribution statement

Jorge Poveda: Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Óscar Santamaría:** Writing – review & editing. **Jorge Martín-García:** Writing – review & editing. **Daniel Martín-Jiménez:** Writing – review & editing, Writing – original draft, Visualization, Investigation.

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.

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Data availability

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

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