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REVIEW ARTICLE

Harnessing the multifaceted benefits of probiotics: A sustainable strategy to combat the post-harvest diseases inciting perishable products

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Abstract

Post-harvest management plays a vital role in agricultural food chains, especially in developing countries, as it focuses on maintaining the quality and shelf life of the produce while minimizing losses. Post-harvest loss (PHL) refers to reducing food quantity and quality from harvest until it reaches consumers. Among the various factors contributing to PHL, the losses due to disease are detrimental. They lead to spoilage through symptoms such as rotting and the production of harmful toxins. Due to its perishable nature, fruit and vegetables are most vulnerable to various post-harvest pathogens. Chemical fungicides are commonly used to manage post-harvest diseases, but they pose risks of environmental pollution, consumer health concerns and pesticide resistance by pathogens. To overcome the negative impact resulting from the use of chemical compounds, there is an urgent need to develop alternate control measures for protecting perishable produce and human health. Recently, beneficial organisms have gained a significant role in managing these diseases, with probiotic bacteria and yeast as key organisms. They help to maintain the quality of fresh produce by protecting it from harmful pathogens through rapid colonization, competition for space and nutrients, creation of an acidic environment, activation of defence mechanisms and production of antimicrobial compounds such as cell wall-degrading enzymes, bacteriocins and volatile organic compounds. Probiotic-based treatments were applied through edible coatings, sprays, or incorporated into packaging materials as natural and safe ways to extend the shelf life of perishable goods. This review prioritized compiling research findings employing the mechanism of probiotics in disease management and its utilization for managing post-harvest diseases.

Keywords

antimicrobial; food security; health benefits; post-harvest diseases; probiotics

Introduction

India, a sub-tropical country with diverse agro-climatic conditions, is a leading producer of various agricultural and horticultural commodities. However, the significant issue of post-harvest losses adversely impacts its economic status. Among these commodities, fruits and vegetables, due to their perishability, are highly susceptible to post-harvest losses, ranging from 30 %

to 50 % (1). In particular, horticultural crops pose substantial challenges post-harvest during storage. Post-harvest fungi are the primary agents responsible for spoilage (2). Globally, 20-50 % of post-harvest losses in horticultural crops are attributed to fungal and bacterial diseases (3). These losses reduce food availability, threaten food security and have dreadful economic consequences, especially for small-scale farmers and local economies. It is widely found that fungi play a significant role in post-harvest spoilage, causing extensive damage during storage by spreading from lesions produced during harvesting, ultimately affecting entire lots of produce. Post-harvest losses of fruits and vegetables are primarily due to inadequate maintenance techniques during harvesting, transportation, storage and distribution (4). The freshness of these produce after harvest is influenced by factors such as water content, respiratory rate, ethylene production, and endogenous plant hormones, as well as external factors like microbial growth, temperature, relative humidity, and atmospheric conditions.

Post-harvest diseases in agriculture and food production represent a formidable challenge, as they encompass a broad spectrum of microbial infections, physiological issues and decay processes that impact crops and stored agricultural products from the field to the consumers' table. These challenges underscore the critical need for effective strategies to combat post-harvest losses and ensure the availability of high-quality, safe and nutritious food. It is vital to control post-harvest diseases to address these losses and preserve sound quality. Control methods encompass biological, chemical and physical treatments (5). Biological therapies involve bioagents, essential oils and botanicals.

In contrast, chemical treatments include antibiotics and fungicides and physical therapies employ heat treatments (hot water, vapour heat), cold storage, irradiation and modified/controlled atmospheres (6, 7). However, the use of therapeutic fungicides as pre-harvest treatment in field conditions poses a serious concern due to the potential residues of these chemicals on consumable products, leading to restrictions on their use worldwide (8). Consequently, there is a compelling demand for developing substitute intervention methods focusing on mitigating the disease prevalence and ensuring the safety and quality of agricultural produce (9).

Biocontrol methods represent a promising avenue in the fight against post-harvest diseases. These methods harness the power of beneficial microorganisms, such as certain bacteria and fungi or natural compounds derived from plants, to combat pathogens responsible for post-harvest spoilage (10). Unlike traditional chemical treatments, biocontrol agents offer several distinct advantages. They are environmentally friendly, posing minimal risks to ecosystems and reducing the potential for harmful chemical residues on food products (11). Moreover, they are often precise in targeting pathogenic microorganisms, minimizing collateral damage to non-target species. Recently, probiotics have gained importance as a captivating and revolutionary approach to biocontrol in managing post-harvest diseases, primarily because they are safe for human consumption and have no adverse effects (12). This review focuses on gathering studies about probiotics, where they come from, their key traits and how they help to manage post-harvest diseases. Relevant publications were sourced from Google Scholar, using terms like "probiotics," "post-harvest diseases," and "biocontrol." The selected studies addressed the probiotics' role in combating post-harvest diseases.

Post-harvest diseases: Losses and their impact on human health

The moment crops are harvested, they are at risk. Fruits, vegetables and grains become susceptible to numerous microbial pathogens. These invaders, primarily fungi and bacteria, can access produce through natural openings, wounds, or weakened tissues, leading to rapid deterioration during storage, transportation and eventual marketing (13). Post-harvest losses caused by pathogens in perishable produce account for millions of dollars every year (14). According to Food and Agriculture Organization (FAO) data, about one-third of all the food produced for human consumption, equivalent to 1.3 billion tons, is wasted or lost annually (15). "Food loss" is defined as available food for human consumption goes unconsumed. Here, post-harvest loss includes food loss from harvesting until consumption. Post-harvest loss accounts for direct physical and quality losses that reduce the economic value of the crop or may make it unsuitable for human consumption. A significant portion of this massive wastage can be attributed directly to post-harvest diseases. This phenomenon is particularly noticeable in developing countries where the lack of advanced storage facilities intensifies the issue. The quality degradation of post-harvest products leads to a tangible reduction in their nutritional profile (16).

Fungal infections caused by species such as *Botrytis cinerea*, *Aspergillus*, *Penicillium*, *Sclerotinia*, *Monilinia, Colletotrichum* and *Fusarium* pose significant challenges due to their ability to cause latent infections and produce harmful toxins. These pathogens can severely compromise the quality and safety of a wide range of fruits, vegetables and grains, leading to substantial losses in agricultural produce (17). For instance, *Penicillium* species, like *P. digitatum* and *P. italicum*, are highly notorious for citrus, pome (like apples and pears) and stone fruits (like peaches and plums). After harvesting, they are behind the nasty rotting, turning fruits soft, watery and mouldy. These moulds fasten their spread in warm, humid storage spaces, sneaking into fruits through minor cuts or bruises and can destroy whole batches of fruits, leading to significant losses. These fungi are behind 60-80 % of losses in citrus fruits due to decay (18).

On the other hand, *Aspergillus flavus* poses a dual threat: while it affects commodities like peanuts and maize, it produces mycotoxins, namely aflatoxins—potent carcinogens detrimental to human health. In addition, these post-harvest pathogens are reported to produce harmful mycotoxins, resulting in deleterious effects on humans (19). Furthermore, the fungus *Botrytis cinerea*, responsible for the dreaded grey mould, is a ubiquitous pathogen that threatens a variety of fruits and vegetables post-harvest (20). Furthermore, the consumption of mold-infested produce has been linked to allergic reactions, respiratory complications and even food poisoning (21). Bacterial pathogens like *Erwinia*, *Pectobacterium* and *Dickeya* can cause soft rot in numerous fruits and vegetables. These bacteria not only cause rotting but also degrade essential nutrients, reducing the health benefits of the affected produce and resulting in yield loss ranges between 15 and 30 % (22). Furthermore, secondary invaders in the rot might produce toxins. Combined with the economic consequences of reduced yield and increased prices, soft rot can indirectly impact overall diet quality and access to nutritious foods.

Biocontrol agents: An alternative to chemical management

Conventional post-harvest disease management practices highlight careful harvesting to prevent injuries that invite infections and the removal of infected regions on produce. Clean storage facilities, maintained with agents like $CuSO_4$ and formaldehyde, reduce contamination risks. Cold storage and transport slow disease progression, while good ventilation in storage further curbs disease spread. Keeping crops pest-free avoids new wound formations and treatments like hot water and air further control disease. Chemical control, using substances like thiabendazole and dicloran, has traditionally been vital for managing post-harvest diseases. However, the use of synthetic fungicides is declining due to environmental concerns, such as water and soil contamination, issues like pathogen resistance, limited fungicide variety and increasing residues in the produce. Beneficial microorganisms, primarily serving as biocontrol agents, have emerged as a viable solution (23). From a safety viewpoint, these agents present a clear advantage: they do not leave harmful residues on food, ensuring that the resulting produce is of higher purity and healthier for consumption. When strategically incorporated into disease management systems, biocontrol agents can provide cost benefits and substantially reduce post-harvest losses. They typically exhibit a minimal ecological impact, pose little threat to non-target species, are biodegradable and don't leave persistent residues (24). Furthermore, specific biocontrol agents have the added advantage of extending the shelf life of agricultural commodities (25). The secretion of antimicrobial substances or outcompeting pathogens for nutrients ensures the produce remains fresh for extended periods (26). Several bacterial, fungal and yeast species have been reported as potential agents to combat post-harvest pathogens (5).

Probiotics: The frontier in post-harvest disease management

"Probiotics," derived from the Greek word "for life," refers to living non-pathogenic microorganisms and their beneficial effects on hosts. The concept was introduced by Vergin, who observed that "probiotika" positively impacted gut microflora during his study of the adverse effects of antibiotics and microbial substances on the gut. Probiotics are live microorganisms that provide health benefits to the host when consumed in adequate amounts, primarily by supporting a balanced gut microbiota (28). The use of probiotics in post-harvest disease management dates back to the late 20th century when researchers started exploring alternatives to synthetic fungicides. Drawing inspiration from the success of beneficial microorganisms in other fields, scientists investigated their potential against post-harvest pathogens. During the 1980s and 1990s, efforts were directed at isolating and studying beneficial microbes from healthy fruit and vegetable surfaces, such as yeast and bacteria. Over the years, various strains have been commercialized, with applications spanning a range of crops and post-harvest diseases. Widespread probiotic microorganisms include *Lactobacillus rhamnosus, L. reuteri,* certain strains of *L. casei*, *L. acidophilus*, *L. salivarius*, *L. plantarum*, *L. paracasei*, *Bifidobacteria*, *Bacillus coagulans*, *B. lactis*, *B. masentericus*, *Enterococcus faecium*, *Streptococcus facealis*, *Clostridium butyricum* and some edible yeast species like *Saccharomyces boulardii* (29, 30) (Fig. 1).

These probiotics are commonly added to foods, especially fermented milk products, individually or in combination. As the probiotics are consumed orally and benefit human health, their presence in consumable fruits will not harm humans. When applied to harvested produce, these beneficial microorganisms can competitively exclude harmful pathogens, preventing their establishment on produce surfaces. Furthermore, certain probiotics produce antimicrobial substances like bacteriocins and organic acids, which can deter the growth of spoilage-causing pathogens, thereby extending the freshness and safety of the produce (31, 32). All these factors collectively make probiotics an appealing and effective solution for managing post-harvest diseases.

Health Benefits of Probiotics in Human

Probiotics, known as beneficial bacteria, offer diverse health benefits (33). They support gut health by aiding digestion and nutrient absorption and strengthening the intestinal lining, with some strains alleviating digestive issues like irritable bowel syndrome (IBS) (34). Beyond digestion, probiotics enhance immunity against various infections and show the potential to improve mental health by influencing the gut-brain axis (35). They assist in managing cholesterol, combating antibiotic resistance and alleviating food sensitivities. Probiotics promote womens' health, improve skin conditions and support cardiovascular health. Recently, studies have hinted at the potential of probiotics in offering adjunctive treatment for non-alcoholic fatty liver disease and even supplementing diabetes management (36). Collectively, these insights reinforce probiotics as pillars of preventive health and holistic well-being.

Characteristics of probiotics

Probiotics must confer health advantages to the host when consumed in adequate amounts. A strain must meet specific vital criteria to be officially recognized as a probiotic. The most essential requirement is safety. Probiotics

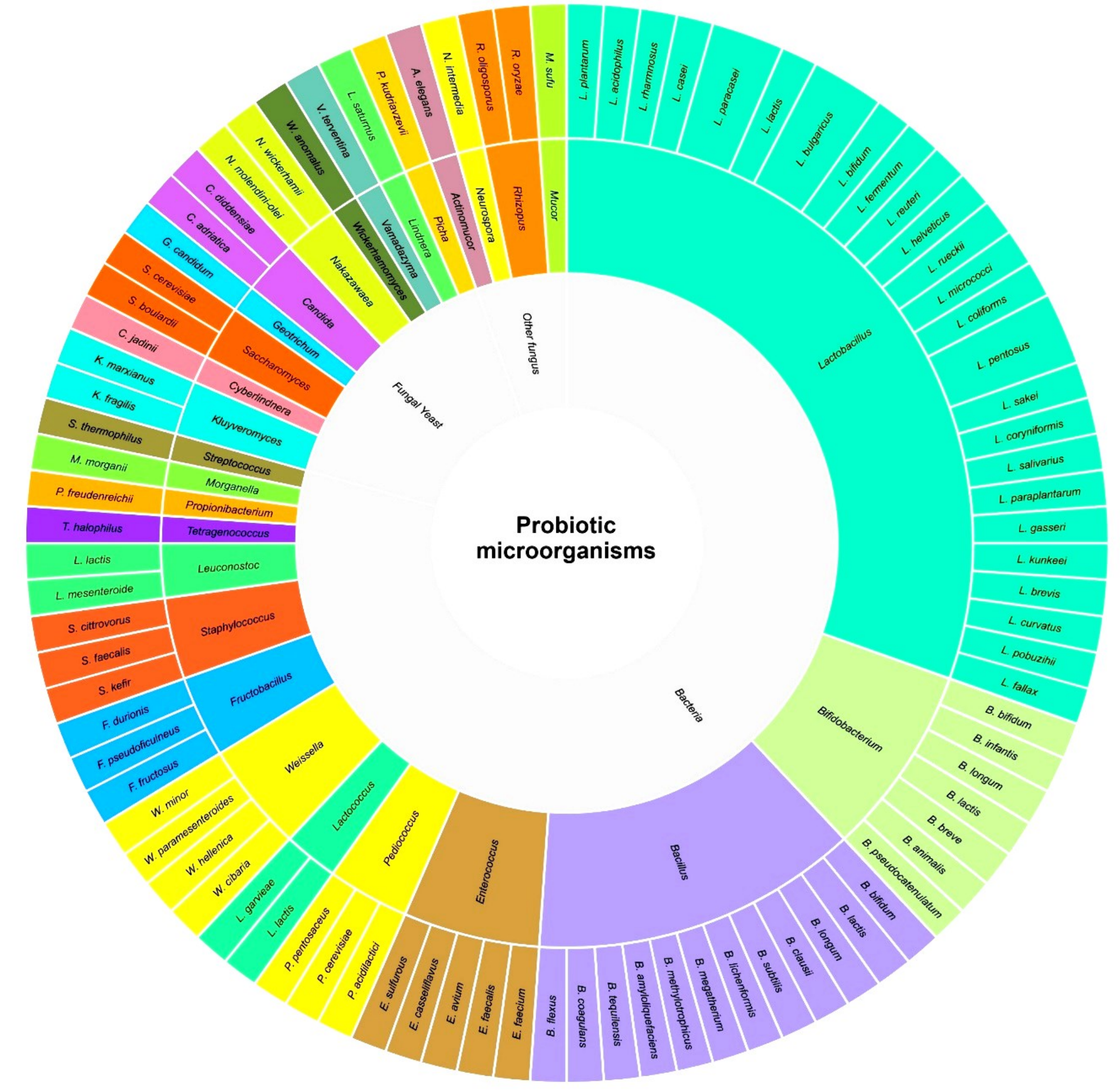

Fig. 1. Taxonomic circular visualization of probiotic microorganisms.

should be inherently safe for consumption, non-pathogenic, non-toxic and free from genes that could spread antibiotic resistance (37). This is important because humans regularly consume probiotics as supplements or in foods like fermented products. They must remain stable and viable under storage and field conditions. It should be able to survive (not necessarily grow) in the intestine. Once consumed, they must endure various challenges, especially during their journey through the digestive system. They must be stable and capable of withstanding the acid and bile environments of the stomach and small intestine, both of which can destroy bacteria (38).

Probiotics don't need to grow in the gut, but they need to reach the large intestine (colon) in good condition to have positive effects. They should fight harmful bacteria by producing substances that inhibit their growth or compete with them for nutrients and space in the gut. They should also strengthen the immune system, fight infections, and reduce inflammation. Additionally, probiotics help maintain the gut lining, preventing harmful substances and bacteria from leaking into the bloodstream, which can cause various health issues. In summary, for a microorganism to be a true probiotic, it must be safe to consume, able to survive storage and digestion, capable of sticking to the gut and effective at supporting health by boosting immunity, fighting harmful bacteria and protecting the gut lining. These qualities ensure that probiotics provide real and lasting benefits (39).

Probiotics sources

Probiotics are essential for maintaining a healthy balance of gut microorganisms and overall well-being. They can be found in various natural sources within the human body, such as dairy products and certain fermented and non-fermented foods (Fig. 2). They naturally occur in breast milk, saliva, and the gut (40). In addition, probiotics are

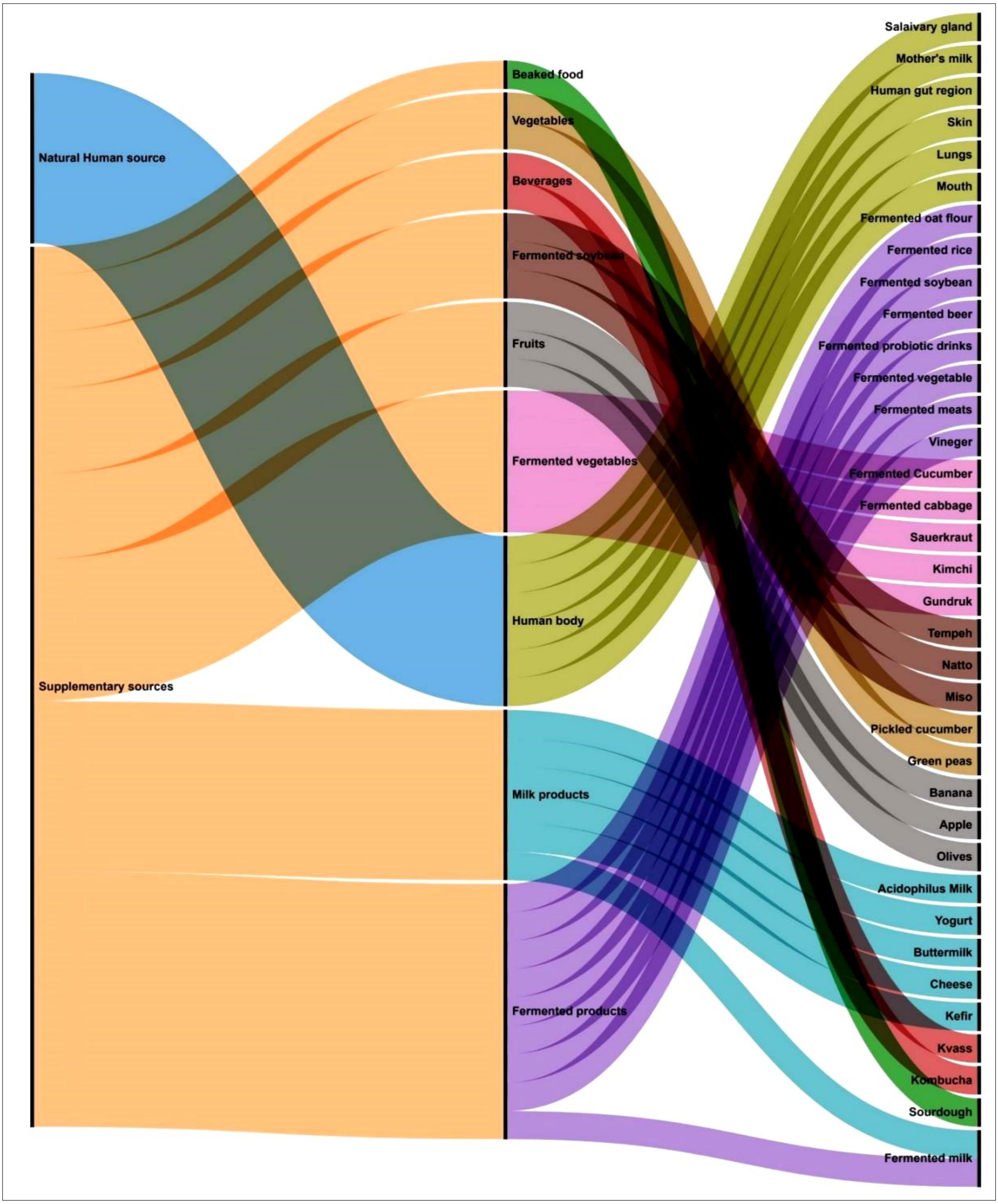

Fig. 2. Probiotic diversity: visualizing natural and supplementary sources.

abundant in fermented foods, which provide diverse dietary options and promote digestive health. Fermented dairy products like yoghurt and kefir are well-known sources. Yoghurt is prepared by fermenting milk with lactic acid bacteria and *Bifidobacteria* (41), while kefir combines milk with Yeast and bacteria cultures (42). Traditional buttermilk, a by-product of butter production, is another natural probiotic source valued for its digestive benefits (43). Fermented soy products such as tempeh, natto and miso also offer probiotics. Tempeh is a soybean-based food with a nutty flavour, while natto contains the *Bacillus subtilis* strain. Miso, fermented with koji fungus, is widely used in Japanese cuisine, especially in soups (35, 44, 45). Vegetable-based fermented foods include kimchi and sauerkraut. Kimchi, a Korean dish made with cabbage and seasoned with spices, sometimes includes ingredients like radishes or carrots. Sauerkraut, fermented from finely shredded cabbage, is another excellent source of probiotics. Probiotic beverages such as kombucha, a fermented tea made with bacteria and yeast cultures, also provide health benefits (46). Incorporating these natural probiotic-rich foods and drinks into daily meals can enhance gut health and overall wellness.

Mechanism of probiotics in post-harvest disease management

Probiotics combat harmful pathogens through various mechanisms (Fig. 3) (12). One significant way they achieve this is by producing organic acids like lactic acid and acetic acid during sugar fermentation. These acids create an acidic environment, inhibiting harmful bacteria growth. When these acids penetrate pathogen cells, they disrupt the internal pH balance, ultimately killing them. Some organic acids, mainly citric acid, chelate metal ions (e.g., calcium and magnesium), destabilize pathogen cell walls. It also interferes with quorum sensing in pathogens, disrupting their ability to coordinate infection strategies. Probiotics also generate secondary metabolites such as ethanol, acetaldehyde and acetoin, small molecules with low molecular weight that inhibit the pathogens' growth and disrupt their cell membranes.

Additionally, many probiotics produce bacteriocins—protein-based compounds with antibiotic-like properties. These substances (Lactacin B, Nisin, Plantaricin & bifidocinB) inhibit harmful bacteria's cell wall synthesis by disrupting their structure or creating pores (47). While some bacteriocins target specific bacteria, others have a broader host range, effectively battling foodborne pathogens. Another antimicrobial property involves producing hydrogen peroxide, particularly by lactic acid bacteria, through enzymatic reactions. Even a lower concentration of hydrogen peroxide can disrupt essential proteins and enzymes on the surface of pathogens, leading to their destruction. Probiotics further protect the harvested produce by competing with pathogens for nutrients and space. They can break down toxins released by harmful bacteria and block these toxins from binding to host cells. In addition to these mechanisms, probiotics produce lytic enzymes such as phytases, murein hydrolases, chitinases, cellulases and glucanases. These enzymes are involved in degrading complex structures like cell walls of pathogens and help eliminate them. They also produce siderophores, which bind to iron in the environment, depriving harmful microbes of this vital nutrient and impeding their growth. Organic acids and siderophores contribute to biofilm production, forming a physical barrier on produce surfaces that prevents pathogen colonization (31, 32, 48). Recent research has uncovered even more ways probiotics work.

Antagonistic potential

The antagonistic potential of lactic acid bacteria

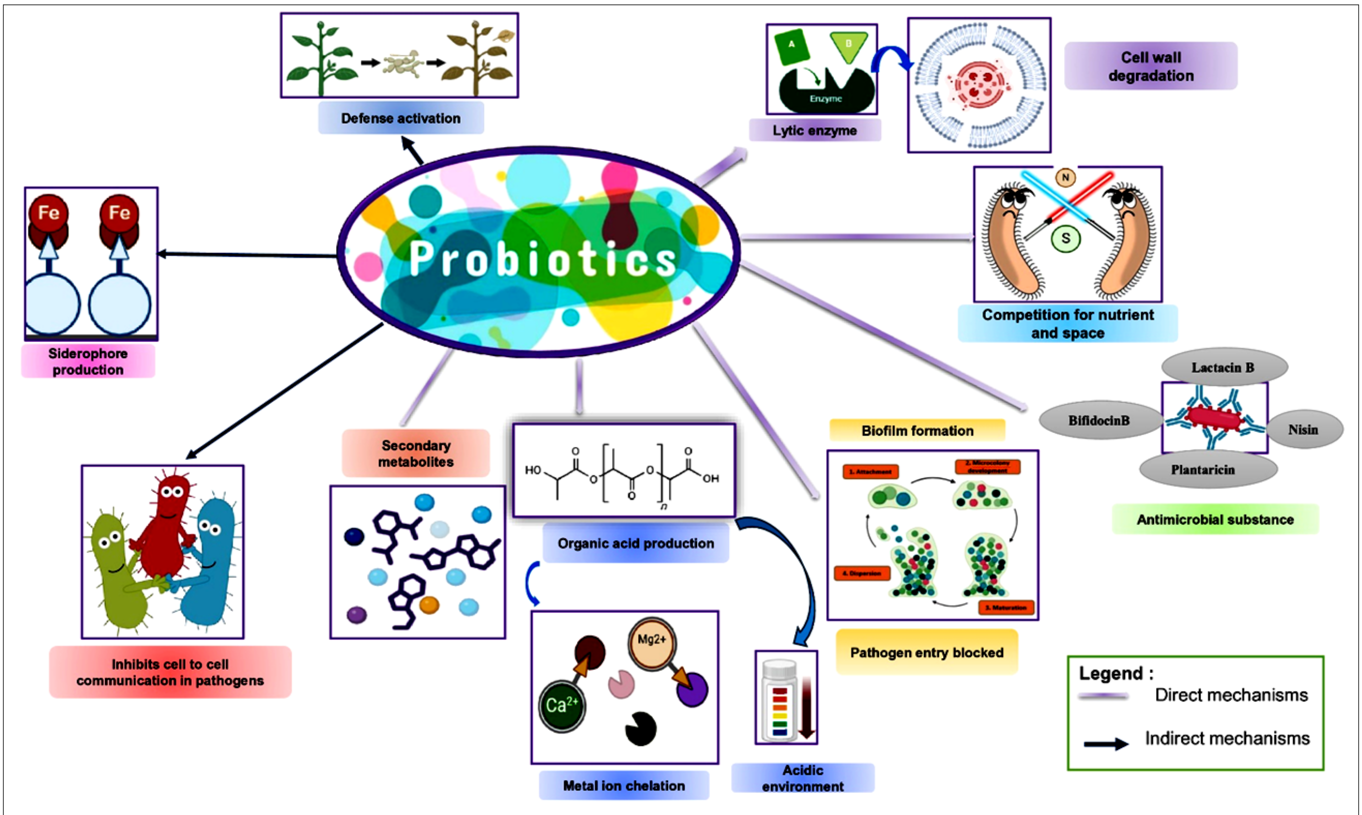

Fig. 3. Infographic representation of mechanisms of probiotics against post-harvest diseases.

Lactic acid bacteria (LAB) are emerging as promising agents in post-harvest disease management of fruits and vegetables. Their ability to combat pathogenic microbes is mainly due to the production of antimicrobial compounds and peptides (bacteriocins). These metabolites encompass various compounds, including hydroxy derivatives of fatty acids (e.g., palmitic, stearic, oleic and linoleic acids), organic acids (e.g., phenyl lactate, lactic, acetic and propionic acids) and cyclic dipeptides (diketopiperazines) (49).

Recent studies have highlighted the inhibitory potential of *Lactiplantibacillus plantarum* strains isolated from fruits and vegetables against the growth of *Botrytis cinerea.* These strains inhibited fungal growth in fresh-cut kiwifruit , table grapes and Strawberries (52). This antifungal activity is believed to result from producing antimicrobial secondary metabolites. The effectiveness of incorporating the *Lactiplantibacillus plantarum* A6 into an edible coating based on exopolysaccharides from *Weissella confusa* JCA4 (53). This approach was notably effective in controlling the growth of spoilage and pathogenic fungi such as *Aspergillus niger*, *Fusarium* sp. and *Rhizopus stolonifer* in cherry tomatoes. Similarly, in citrus fruits, the green and blue mould fungus (*Penicillium digitatum* and *P. italicum*) was found to be controlled using LAB strains such as *L. paraplantarum* CRL 1905, *L. fermentum* CRL 973, *L. casei* CRL 1110 and *L. reuteri* CRL 1101(54).

Beyond pathogenic fungal control, LAB strains have shown detoxifying properties against harmful toxins, viz., aflatoxin and ochratoxin. For instance, the ochratoxin-A detoxifying potential of *Pediococcus pentosaceus* strains in grapes fruits is mainly due to the production of organic acids (55). Additionally, treating almonds and peanuts with *L. kefiri* FR7 significantly delayed the *Aspergillus* growth. It reduced the concentration of aflatoxins by 85.27 % (AFB1) and 83.94 % (AFB2) in almonds, as well as decreased ochratoxin -A (OTA) production by 25 % in peanuts (56). Furthermore, *Limosilactobacillus fermentum* strains show inhibitory against *A. flavus* and *A. niger*, leading to a reduction in aflatoxin (AFs) and other food contaminants (57).

The antagonistic potential of Bifidobacterium

Bifidobacterium is widely recognized for its health-promoting properties in the human gut. Its application in post-harvest disease management is attributed to its inherent antibacterial properties. Specific strains, such as *B. bifidum* NCFB 1454, are known to produce unique antimicrobial compounds, including bifidocin B (58). The use of Lacticaseibacillus casei and Bifidobacterium animalis subsp. lactis incorporated into alginate-based prebiotic coatings for fresh blueberries (59). These coatings effectively maintained the fruits' quality (colour and firmness) and sensory characteristics throughout their shelf-life.

The antagonistic potential of Bacillus species

Bacillus species have emerged as versatile and efficient probiotics with a notable timeline of success in both agricultural and medical fields. The efficacy of *Bacillus-derived* bio fungicides against apple blue mould, establishing their role in mitigating post-harvest diseases (60). For instance, research indicates its potential in controlling potato soft rot and its role in managing tomato post-harvest rot (61, 62). These milestones underscore *Bacillus* significance in promoting food security and human health through its multifaceted applications.

The antagonistic potential of yeast

Recent research highlights the potential of yeasts, traditionally known for other roles, as biocontrol agents in agriculture. A study focused on yeasts from kimchi, a Korean fermented dish, identified ten out of 90 strains with potent antifungal properties. *Pichia sp., Kluyveromyces marxianus, Yarrowia lipolytica* and *Issatchenkia orientalis* exhibited notable biocontrol effects. *Pichia kudriavzevii* stood out for its multifunctional defence strategies, which include forming biofilms and emitting volatile compounds. Meanwhile, *Kluyveromyces marxianus* demonstrated wound colonization and induced plant resistance and *Yarrowia lipolytica* countered pathogens through enzyme production and mycelia adhesion. Research indicates the growing role of yeasts in sustainable post-harvest management (63). The occurrence of several yeasts, such as *Saccharomyces sp., Candida sp., Debaryomyces sp., Kluyveromyces sp. and Yarrowia sp.,* in various Indian fermented dairy and dairy-related products like curd, cheese, idli, dosa, jalebi, warries, pappad, kanji, fruit juices, bakery products and brewery products have been reported. Renowned for its role in brewing and baking, Saccharomyces cerevisiae has emerged as a potential defender against post-harvest diseases (64).

Studies have highlighted its effectiveness in counteracting *Botrytis cinerea* on crops such as grapes and strawberries (65). The underlying mechanisms through which Saccharomyces cerevisiae yeast operates involve competing for essential nutrients with the pathogen and producing antifungal compounds that inhibit the growth of the pathogens (66). Another yeast, *Aureobasidium pullulans,* has been successfully employed against a spectrum of post-harvest pathogens, especially in fruits like apples and citrus, providing an environmentally friendly approach to combating spoilage (67). The yeast *Metschnikowia fructicola* has also drawn attention to safeguarding various fruits. It has shown promise as a biocontrol agent against post-harvest pathogens in fruits such as strawberries and peaches. The capabilities of *Pichia membranifaciens* have been explored in post-harvest disease management, where it has been evaluated for its efficacy against the challenging pathogen Botrytis cinerea on kiwifruit (68). Furthermore, *Starmerella bacillaris* (previously recognized as *Candida zemplinina)* has showcased potential against post-harvest apple decay, opening avenues for its use in broader applications (56). Reinforcing the versatile role of *Saccharomyces cerevisiae,* studies have amplified its significance beyond brewing and baking, demonstrating its capability in biocontrol, especially against fungal infections in post-harvest fruits saravana (69).

Advances in probiotic delivery for controlling post-harvest disease

Probiotics have emerged as a promising approach for post -harvest disease management in fruits and vegetables, offering sustainable alternatives to chemical antimicrobial treatments (Table 1). One innovative technique is biofumigation, where storage environments are saturated with volatile organic compounds (VOCs) produced by probiotics, creating an inhospitable atmosphere for pathogens. However, despite their potential benefits, the efficacy of probiotics can be variable and influenced by factors such as environmental conditions, crop types and the specific disease targeted (24). Researchers are exploring integrative approaches that combine probiotics with other post-harvest treatments to address these challenges. For instance, modified atmosphere packaging can be synergistically employed with probiotics to provide consistent and enhanced results in disease control (70). These holistic

Table 1. Probiotic agents for post-harvest pathogen control: mechanisms and host applications

S. No.	Probiotics / along with edible coatings (or) supplements.	Sources	Post-harvest pathogen	Host	Mechanisms involved	References
1.	Killer yeast – *Debaryomyces hansenii* K12a & *Wickerhamomyces anomalus* BS91	Blue-veined Rokpol cheese & fermented olive brine	Brown rot – *Monilinia fructigena* and *M. fructicola*	Peach and Plum	Effective colonization & Biocontrol activity – production of hydrolytic enzymes, killer toxins and volatile organic compounds.	(76)
2.	*Metschnikowia pulcherrima*	Wild apple	*Penicillium expansum*	Apple	Competition & production of an antimicrobial compound – pulcherrimin. Detoxification of patulin.	(77)
3.	*Bacillus subtilis and saccharomyces cerevisiae* + *Chinese herbs*	-	*Penicillium digitatum*	Citrus	Inhibitory effect, accumulation of defence enzymes and promotes the quality of fruits.	(78)
4.	Killer yeast - *D. hansenii* KI2a and *W. anomalus* BS91 strains	Blue-veined Rokpol cheese & fermented olive brine	*Monilinia fructicola*	Apple fruits	Host defence activation – induction of defence-related enzyme.	(79)
5.	*Meyerozyma* sp. 1 &2, *Saccharomyces* sp and *Bacillus* sp. 3	Milk products – kefir grains	Penicillium rot	Apple and grapefruit	Antagonistic activity – reduced disease incidence	(80)
6.	*Debaryomyces hansenii*	-	*Colletotrichum gloeosporioides*	Papaya	Antagonistic activity - Volatile organic compounds (VOCs) production, β-1, 3 glucanase and protease activity, inhibition of spore germination and competition for nutrients.	(81)
7.	*Lactobacillus acidophilus*	Healthy unripe mango	*C. gloeosporioides*	Mango	Antagonistic activity – Production of antifungal compounds and lytic	(82)
8.	*L. plantarum* 020 and *L. acidophilus* 016	-	Post-harvest fungal and bacterial pathogen (storage)	Carrot	Reduced the contamination and maintained the physicochemical properties of carrots	(83)
9.	Lactic acid bacteria and Yeast isolates.	Curd, fermented dosa material, fermented jowar and bajra flour	*Colletotrichum* and *Alternaria*	Mango	Inhibitory effects and increased TSS content as well as the shelf life.	(84)
10.	*L. plantarum* A7 + essential oils (Cumin/ Thyme)	-	Gray mould rot – *Botrytis* sp.	Strawberry	Inhibitory effects and quality maintenance.	(85)
11.	Lactic acid bacteria and Yeast isolates	Curd, fermented dosa material, fermented jowar and bajra flour	*Rhizopus* sp. and *Alternaria* sp.	Grapes	Inhibitory effects- unidentified mode of action	(86)
12.	Lactobacillus strains fermented agricultural by-products (cell-free supernatant)	-	*C. gloeosporioides* and *Botryodiplodia. theobroma*	Mango	Inhibitory effects and maintained the post-harvest quality	(87)
13.	*Saccharomyces cerevisiae, Wickerhamomyces anomalus, Metschnikowia pulcherrima* and *Aureobasidium pullulans*	Fermented olive brine and minimally processed pomegranate	*Botrytis cinerea*	Grapes	Multiple modes of action: colonization of wound, competition for iron, biofilm formation and production of hydrolytic enzymes & volatile organic compounds	(68)
14.	*L. plantarum* CM-3	Healthy strawberry fruit	*Botrytis cinerea*	Strawberry	Effective colonization on wound site and inhibitory effects.	(88)
15.	*L. plantarum* CM-3	-	*Botrytis cinerea*	Grapes	Enhance host resistance – alter the expression of defence-related genes.	(89)
16.	*Lactiplantibacillus plantarum strains* UFG 121 & PAN01 (cell free supernatant)	-	*Botrytis cinerea*	Fresh-cut kiwi fruits	Organic acid production and lower pH.	(50)
17.	L. *plantarum* subsp. *Plantarum* strain ATCC 14917 + edible coating with potato starch and sodium caseinate	Pickled cabbage	*Botrytis cinerea* strain CECT 20518	Table grapes	Early colonization of fruits, competition and antifungal activity improve fruit quality.	(62)
18.	*B. amyloliquefaciens* LPB-18	Earthworm	*Aspergillus flavus* and *Fusarium oxysporum*	Foodborne pathogens	Production of antibiotic compounds- Fengycin A and B	(90)

19.	*Lactiplantibacillus plantarum* MYSAGT3	Traditional herbal juice	*ochraceus*	-	Antifungal activity – organic acid production	(91)
20	*L. kunkeei ENH01*	Unpasteurized natural honey	*A. niger* and *Candida albicans*	-	Antibacterial peptides and antifungal activity	(92)
21	*Saccharomyces cerevisiae* CR-1	Fermentation process for fuel production	citrus black spot - *Phyllosticta citricarpa*	Citrus	Volatile organic compounds	(93)
22.	*Hanseniaspora opuntiae L479* and *Metschnikowia pulcherrima L672*	Fig crop	*Penicillium expansum, Cladosporium cladosporioides, Monilia laxa* and *Botrytis cinerea*	Decayed figs and Breba crops	Inhibitory effects on spore germination and mycelial growth	(94)
23.	Alginate biofilm coating of *W. anomalus* and *Pichia membranifaciens LW26*	Apple fruit	*Botrytis cinerea* and *Penicillium italicum*	Apple fruits	Inhibitory effects – unidentified mode of action	(95)
24.	*Metschnikowia pulcherrima* Mp-22 and Mp-30 strains	Grapes fruit	*Alternaria alternata, Botrytis cinerea* and *Penicillium expansum*	Post-harvest pathogen	Antifungal metabolites production	(96)
25	*Bacillus subtilis* SB8 + alginate edible coating	Healthy strawberry fruit	*B. cinerea*	Strawberry	Antimicrobial compounds and competition for space and nutrient	(2)
26.	*Pichia kudriavzevii* (M74) microencapsulated with sodium alginate and cornstarch	Citrus tree	*P. digitatum* and *P. italicum*	Orange	Lytic enzyme production	(97)
27.	*Lactobacillus farciminis* LJLAB1		*P. carotovorum*	Pepper	Antibacterial activity- Bacteriocin production	(27)

strategies aim to optimize probiotics utilization while preserving fresh produce's quality and safety. In parallel, various probiotic application methods, including direct application, edible coatings and spray drying, demonstrate the adaptability and versatility of probiotics in enhancing product storability while minimizing reliance on chemical treatments. The direct application of probiotics to produce surfaces remains straightforward but requires addressing challenges related to sensory changes and probiotic viability during storage (71).

Edible coatings are well-known for their multifunctional role in preserving fruit quality, enhancing shelf life and being safe for human consumption. Recent studies emphasized their innovative role as a medium for delivering probiotics and bioactive compounds. Commonly used materials for these coatings include alginate (often combined with chitosan and prebiotics), potato starch, corn starch, Sodium alginate, xanthan gum-based and carboxy methyl cellulose. In addition, to improve adhesion and effectiveness, additives such as glycerol, inulin, oleic acid and calcium chloride (CaCl2) are incorporated. This combination helps enhance the survival of probiotics in fruits (7, 72, 73). For example, Potato starch edible coatings infused with *Lactobacillus plantarum* potentially reduced the incidence of grapes *Botrytis,* while Sodium caseinate coatings showed high survival rates of LAB (62). Similarly, research indicates the combined application of alginate and *Bacillus subtilis* SB8 significantly reduced the incidence of grey mould disease in strawberries compared with the application of bacteria alone (74). Furthermore, innovative techniques like spray drying allow for the development of probiotic formulations tailored for fruit applications (75).

Advantages of probiotic treatment

Once the fruits and vegetables are harvested, they cannot be stored in fresh condition without a protective coating. Uncoated produce is exposed to air, resulting in oxidation, which leads to discolouration, nutrient degradation and off-flavours. Also, high moisture conditions cause pathogens to spoil the produce and become unfit for human consumption. The fruits and vegetables are treated with chemical fungicides, artificial preservatives, wax, and plastic films to overcome this loss. Despite this, their residues persistent in the perishables cause direct impacts on humans (98). Recent protective coatings were aimed at microbial communities (especially probiotics), edible coatings and their combination with essential oils. As research continues to evolve, the diverse probiotic application methods underscore beneficial microorganisms' potential in safeguarding fresh produce's quality and safety throughout the post-harvest journey, contributing to sustainable and environmentally friendly solutions (99). Also, they help to improve the taste and texture of the perishable fruits and vegetables (12). The consumption of probiotics-treated produce provides dual health benefits for consumers from fruits and vegetables and probiotic organisms. They help improve the human gut microbiome, resulting in immune development (100) (Fig. 4).

Conclusion

In conclusion, initially renowned for their gut health benefits, probiotics have become a cutting-edge solution in post-harvest disease management by producing antimicrobial substances to outcompete pathogens and prolong the shelf life and offering an eco-friendly alternative to synthetic fungicides. Over time, probiotics in post-harvest disease management trace a steady evolution from initial research to practical applications. They help combat diseases through multifaceted mechanisms involving producing organic acids, secondary metabolites, bacteriocins, hydrogen peroxide and competition for nutrients. Recent research exploring new probiotic strains and their combinations with edible coatings and essential oils broadening

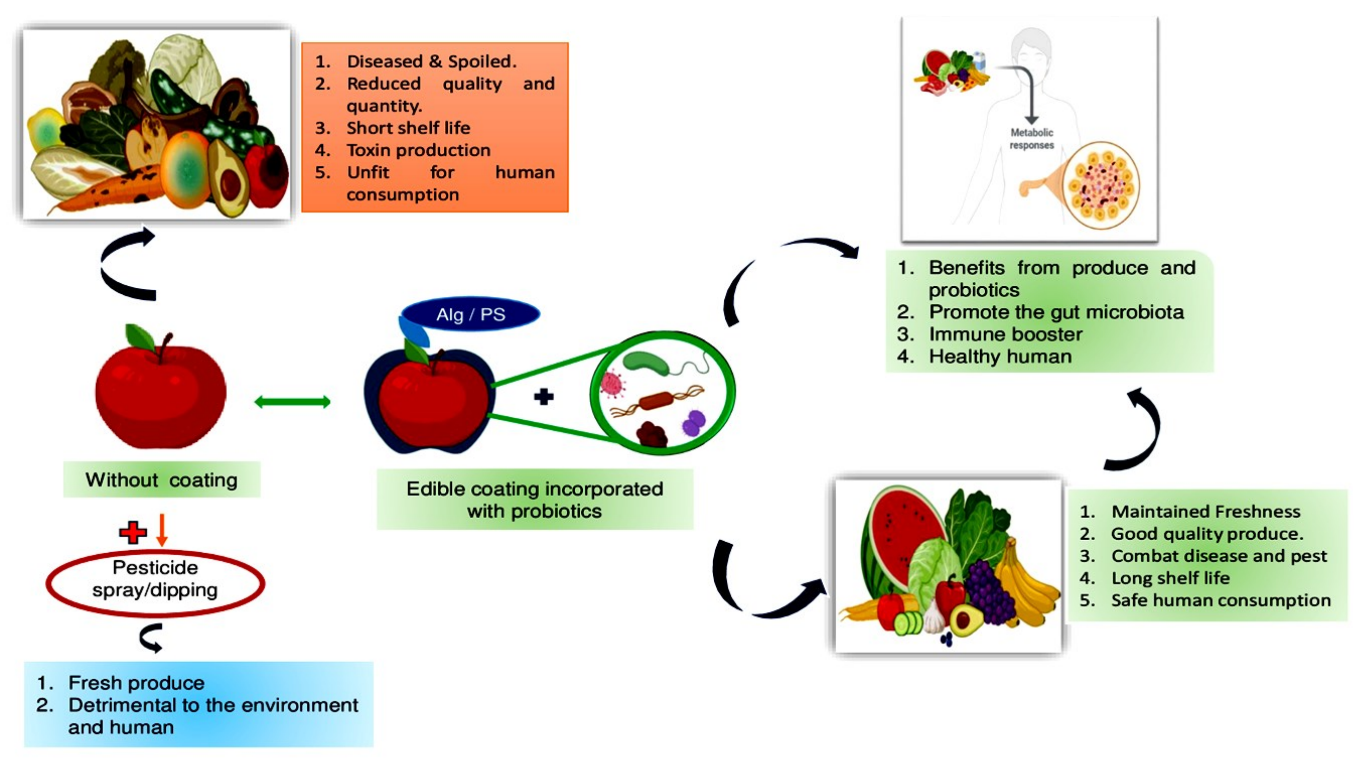

Fig. 4. Potential applications of probiotics and their health benefits.

their potential applications in post-harvest disease management. In essence, probiotics are transforming gut health and are poised to revolutionize agriculture by offering sustainable, safe and effective ways to safeguard our food supply. As we delve deeper into this field, we can anticipate fully harnessing the potential of probiotics to ensure the safety of our harvested produce.

Future perspectives

Probiotics offer sustainable alternative solutions for post-harvest disease management. With consumers' increasing demand for organic and eco-friendly products, probiotics have emerged as a practical approach. Advancements in probiotics formulations and delivery systems must be explored to enhance their effectiveness and stability during storage and transport. For instance, innovative encapsulation techniques and carrier systems could protect perspectives from environmental stress, ensuring their viability and functionality over extended periods. Probiotics integrated with other practices, such as edible coatings or essential oils, can significantly reduce post-harvest losses and improve fruit quality by synergistic effects. Further, they reduce the dependence on chemical fungicides and are environmentally safe.

However, to understand the potentiality of probiotics in post-harvest disease management, advanced omics studies, including genomics, transcriptomics, proteomics and metabolomics, need to be explored. With the help of these tools, the key genes and metabolic pathways involved in the biocontrol properties of probiotics and the impact of environmental factors on their performance can be examined. Further, this also aids in better strain selection, specialized formulations and improved application methods to enhance their efficacy and consistency. Another promising approach involves lacto-fermentation of agricultural by-products, such as palm kernel cake or pineapple peel, which have natural antifungal properties. These offer bio-based solutions to control disease incidence, reduce spoilage and maintain fruit quality during storage. Greater public awareness of the benefits of probiotics in post-harvest management is crucial for their acceptance. In addition, enhancing the regulatory system and addressing legislative challenges will facilitate the commercial development of microbial biocontrol agents. Probiotics have the potential to meet the growing demand for chemical-free, sustainable food preservation. Research into large-scale production and commercialization is essential to make probiotics a promising solution in the agriculture and food industries. Addressing these challenges, the unique benefits of probiotics help extend shelf life and maintain the safety and quality of fresh produce.

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Authors' contributions

SR wrote the original manuscript. AK reviewed and edited the manuscript. TG and KM carried out technical editing. KS and KKK reviewed the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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