FASE FRONTIERS OF AGRICULTURAL SCIENCE AND ENGINEERING
Engineering Transactions of CAE
REVIEW
2026 / Volume 13 / Issue 3 / 25655

Bacterial endophytes in sustainable agriculture: perspectives and advancements as biostimulants and fungal biocontrol agents in crops

Mohammad Jamil KADDOURA, Unnikrishnan KANNAN, Laura AMAYA-QUIROZ, Saji GEORGE (✉)

Department of Food Science and Agricultural Chemistry, McGill University, Ste-Anne-de-Bellevue, Quebec H9X 3V9, Canada.

KEYWORDS

Bacterial endophytes, biocontrol agents, disease management, nanotechnology, plant biostimulants, sustainable agriculture

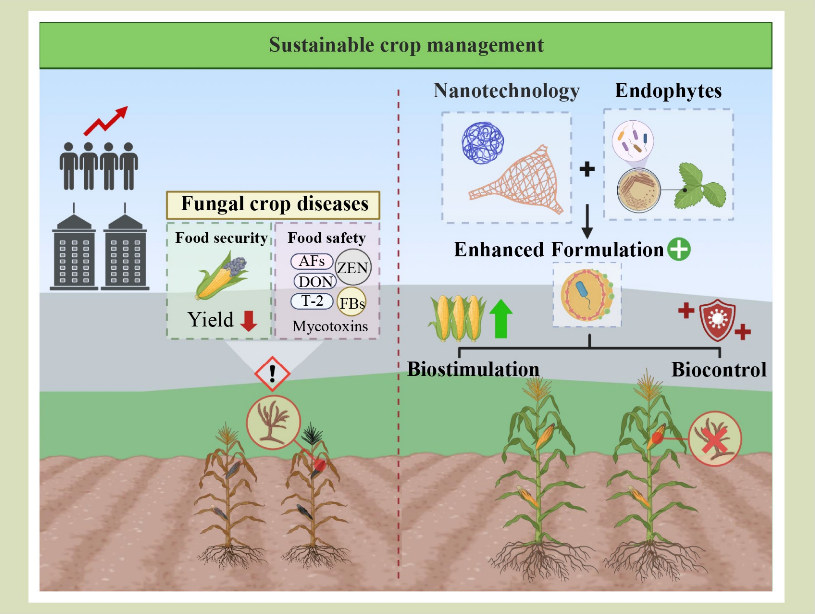
HIGHLIGHTS

- Growing food safety and food security challenges are driven by population growth, limited resources, climate change and plant pathogens, particularly fungi.
- Mycotoxin contamination is an increasing food safety concern, necessitating effective management strategies.
- Bacterial inoculants, including biostimulants and biocontrol agents, offer environmentally sustainable solutions to enhance agricultural production and disease control.
- Overcoming technical challenges in field application by using nanotechnologies will increase the effectiveness and adoption of microbial products.
- Unexamined beneficial endophytic communities are promising as bacterial inoculants since they share traits with plant growth-promoting rhizobacteria and are well-adapted to colonize crops.

Received February 7, 2025;
Accepted August 11, 2025.

Correspondence: Saji.george@mcgill.ca

GRAPHICAL ABSTRACT



ABSTRACT

Agricultural intensification, to meet the nutritional needs of the growing world population, has been made possible through the extensive use of agrochemicals, such as synthetic fertilizers and pesticides. However, these practices pose significant health and environmental risks, including groundwater contamination, soil degradation and microbial resistance. Also, predictions indicate that relying solely on synthetic chemicals to boost production may not be enough to meet the future global need for food. Sustainable agricultural intensification involves the use of novel tools to enhance production while addressing environmental concerns using eco-friendly strategies, such as microbial inoculants. These can improve soil fertility, nutrient cycling and crop yield, while enhancing stress tolerance and overall crop fitness. This review outlines the key aspects of the global presence of plant diseases, plant defense responses and disease management strategies, and examines bacterial endophytes as crop biostimulants and biocontrol agents for sustainable control of mycotoxigenic fungi. It also proposes strategies to increase microbial product adoption by addressing technical limitations, such as field stability, delivery precision and shelf-life.

1 Introduction

Global agriculture stands at a critical juncture, facing the dual pressures of rising food demand and persistent pathogen threats. Current farming methods are not adequate to meet the need to sustain high productivity while minimizing the environmental and health risks associated with conventional agrochemical use. Among the most serious threats to crop performance are plant diseases caused by fungal pathogens, with mycotoxigenic species posing the greatest risk to consumers. Current agrochemical methods are insufficient in addressing the dangers posed by mycotoxigenic fungi, leaving the future of food safety and security compromised. These limitations highlight the shortcomings of chemical-based disease management strategies and the need for effective solutions.

In response, biologically based alternatives are gaining attention for their ability to promote plant health and yield while aligning with ecological and regulatory goals. Beneficial microbes, particularly bacterial endophytes have developed as promising tools capable of suppressing pathogens, enhancing stress tolerance and contributing to plant defense through both direct and indirect mechanisms. Their integration into disease management strategies represents a shift toward more sustainable and holistic approaches to crop protection.

This review examines the global impact of plant pathogens and mycotoxins, fungal infection biology and plant defense mechanisms. It examines established and emerging disease management practices, with an emphasis on plant microbiome and beneficial microbes, particularly endophytic bacteria as effective biological tools for crop enhancement and fungal control. Additionally, advances in nanotechnology and formulation science are appraised for their potential to improve field performance of microbial formulations. Finally, the review seeks to provide insights for key challenges limiting broader adoption and outlines future directions for integrating these microbial tools into sustainable and regenerative agricultural systems.

1.1 Plant pathogen impact and yield losses

Plant diseases caused by certain fungi, bacteria, viruses, nematodes and protozoa result in major production and economic losses. Globally, direct crop losses due to plant pests and pathogens are estimated at 20% to 40% of total production, amounting to about 220 billion USD annually[1,2]. However, these estimates do not account for the short- and long-term effects as well as the indirect impact on food security, public health, economies and the environment[1,2]. Around 83% of plant diseases are caused by fungi with the rest being due to viruses, phytoplasmas and bacteria[3]. Also, fungal pathogens alone destroy 30% of crops, impacting food availability for about 600 million people worldwide, and postharvest losses amount to an additional 10% due to quality reduction[4–6]. Also, filamentous fungi can threaten produce both pre- and postharvest as they pose significant health risks due to toxin production. These findings highlight the shortcomings of current disease management strategies and emphasize the need for effective approaches, particularly against fungal pathogens in order to meet the growing demands for quality assured food production.

1.2 Mycotoxin presence and management

Food contamination by harmful microorganisms and their metabolites is a significant global health concern that is intensified by the complexity of the food supply chain and the increased exposure to contaminants. A major challenge in food safety is the increasing prevalence of plant diseases caused by toxigenic filamentous fungi that produce stable and harmful secondary metabolites known as mycotoxins[7]. Global agricultural crop contamination by mycotoxins was estimated at 25% in 1999 by the UN Food and Agriculture Organization, with cereals, maize, nuts, and rice most affected[8,9]. However, recent estimates place contamination levels at 60% to 80% due to increased production, climate change, and the availability of analytical methods with improved sensitivity[8].

Estimated annual losses attributed to mycotoxins in human food, animal feed and products, and soils total to billions of US dollars[10]. The health implications are a significant challenge, with over 400 mycotoxins currently recognized as harmful[11]. Mycotoxicosis can cause a wide range of adverse effects, from acute symptoms, such as vomiting and abdominal pain, to severe or chronic issues, such as immunosuppression, impaired growth, tumors, coma and even death[12,13]. To minimize these risks, postharvest management focuses on reducing food contamination levels through various decontamination strategies, such as heat treatment, irradiation, cold plasma, mycotoxin binders and chemical treatments[14]. These methods exhibit varied effectiveness dependent on several factors, such as the type of mycotoxin, concentration, particle size and moisture content. Also, the impact of food processing on mycotoxin transformation is not fully understood, and current treatments do not guarantee complete detoxification, as transformed toxins may remain harmful and escape detection[15]. Additionally, impacts of decontamination treatments on food texture, flavor and nutritional content need to be considered. Therefore, prevention through preharvest strategies is likely a more effective approach. This includes using host genetic resistance, agricultural practices and crop protection tactics, including fungicide application, biological control and pest management.

1.3 Need for sustainable management approaches

Pesticides have long been central to disease management and represent the second largest group of synthetic chemicals after mineral fertilizers[16]. However, despite their effectiveness, excessive and unregulated use has raised significant health, agricultural and environmental concerns. Bernardes et al.[17] reported that only 1% of applied pesticides effectively target intended pests, with the remaining impacting non-target organisms including beneficial insects, humans and wildlife. Compounding these risks is the widespread occurrence of multiple pesticide residues in food: a recent EU report found that 44.3% of the tested food samples contained more than one pesticide, while the US Pesticide Data Program reported a similar figure of 57.5%[18]. These findings are particularly troubling given the several health concerns associated with pesticide exposure, including increased risk of diabetes among farmers, respiratory issues, endocrine disruption, and potential mutagenic, carcinogenic, embryotoxic, immunotoxic and neurotoxic effects[19–22]. Similarly, environmental persistence in agricultural soils and groundwater, along with their mobility through leaching, volatilization and runoff, amplifies the ecological risks. These properties contribute to bioaccumulation in non-target organisms, biomagnification through food chains and long-term environmental pollution.

Beyond health and ecological risks, pesticides impose substantial financial burdens that are often overlooked. These include regulatory fees, costs associated with environmental degradation, healthcare expenses and defensive costs, such as increased demand for organic produce. In the USA alone, these hidden costs have been estimated at nearly 40 billion USD annually, potentially outweighing the benefits of pesticide use[23]. Given these concerns, there is a growing emphasis on stricter regulations and the adoption of sustainable solutions that minimize health and environmental risks while maintaining agricultural productivity.

Biological pesticides (biopesticides) have emerged as promising alternatives, now comprise about 10% of the global pesticide market[24]. Their market value is expected to grow from 5 to 15 billion USD by 2029, with a compound annual growth rate of almost 14%[25]. With rapid growth in this sector, their market is projected to match that of synthetic pesticides by the late 2040s or the early 2050s[26]. This is largely attributed to their cost-effectiveness in the long run. For example, integrating bacterial biopesticides into navel orangeworm control programs in almond orchards, improved control from 50% to over 90%, resulting in an estimated 20-fold return on investment[27]. Biopesticides are also significantly cheaper and faster to develop, typically requiring under four years and 3 to 7 million USD, compared to over a decade and about 300 million USD of synthetic pesticides[28].

Despite this promising trajectory, research on biopesticides still lags significantly behind that on synthetic pesticides. For example, between 1985 and 2021, fewer than 5000 scientific publications referenced the term *biopesticide* in the Web Science database, compared to over 130,000 for *pesticide*[29]. Although scholarly interest in biological alternatives is rising, these natural pest control strategies remain inadequately investigated. This underscores both the growing potential of biopesticides and the need for stronger scientific engagement.

2 Fungal infections in plants

2.1 Host penetration

Most pathogenic bacteria, viruses and a few fungal species infect the plant through plant wounds and natural openings, such as stomata and hydathodes[30]. In contrast, many pathogenic fungi can actively breach the plant surface, using both enzymatic and mechanical strategies. These fungi produce a variety of hydrolytic enzymes, primarily pectinases but also cutinases and cellulases, which degrade or modify plant cell wall, thereby facilitating infection[31]. This enzymatic activity softens structural barriers, allowing fungal hyphae to advance through the plant epidermis. In addition to enzymatic degradation, many fungi form specialized infection structures known as the appressoria at the tip of their germ tubes. These structures adhere tightly to the plant surface and generate high turgor pressure, which is used to drive an infection peg through the cuticle and cell wall. The peg, supported by the action of hydrolytic enzymes, breaches the host surface and initiates colonization (Fig. 1)[32]. This dual strategy is especially prominent among biotrophic and hemibiotrophic fungi. However, necrotrophic fungi often use extensive enzymatic degradation and toxin secretion.

2.2 Colonization and infection

To improve their chance of survival within the host, fungal pathogens alter the host physiology and functions through the secretion of phytotoxins. These compounds may kill host cells to serve as a source of nutrients or to appropriate the cellular machinery[32]. For example, *Fusicoccum amygdali*, the causal agent of peach and almond canker, produces the phytotoxic metabolite, fusicoccin, which induces irreversible stomatal opening, stimulates the activity of the plant plasma membrane H^+-ATPase, and results in increased cation uptake, elevated transpiration, uncontrolled water loss and wilting[32–34]. Likewise, *Alternaria alternata* produces a cyclic tetrapeptide tentoxin, which inhibits chloroplast development. It does so by blocking energy transfer of the chloroplast-localized CF_1 ATPase and disrupting the transport of nuclear-coded enzyme polyphenol oxidase, ultimately leading to chlorosis and necrosis[32].

During host infection, pathogen-derived low molecular weight compounds, known as exogenous elicitors, are released. These include proteins, carbohydrates, lipids, cell wall fragments or other molecules, all of which can trigger immune responses by binding to plant receptors, thereby activating defense signaling and inducing necrosis[35]. However, some fungal pathogens, such as the pea pathogen *Mycosphaerella pinodes*, can avoid triggering elicitor-induced responses through the secretion of suppressor proteins, such as supprescin A and B, which occupy recognition sites, thus disrupt signal transduction, and interfere with defense gene activation[36,37].

2.3 Fungal avirulence genes

Plant pathogen interactions are often described by the widely accepted gene-for-gene model, which posits that host resistance (R) genes recognize specific pathogen avirulence genes[38]. R genes encode proteins that recognize avirulence gene products whereas avirulence genes encode effector proteins that may be recognized by the host receptors[39]. Incompatible interactions occur when the avirulence gene is present, triggering host defense responses, such as hypersensitive responses, whereas compatible interactions result when the avirulence gene is absent or mutated, allowing the pathogen to infect and cause disease[40].

Additionally, avirulence genes can also be classified by their specificity to host R genes, cultivar-specific genes interact with R genes in specific cultivars whereas species-specific genes interact with R genes across a species or multiple species. The extracellular nature of avirulence proteins and the cytoplasmic localization of R gene products indicates that fungal elicitors might enter plant cells through the haustorial membrane (Fig. 1)[41]. Also, the structural features of avirulence proteins, such as their cysteine content, are closely linked to their secretion pathways and localization patterns. Cysteine-rich avirulence proteins are typically found in the plant apoplast or xylem, while cysteine-poor avirulence proteins are more commonly associated with haustoria-forming pathogens[42].

3 Plant defense systems

Despite the abundance of fungal pathogens, only a minority succeed in establishing infections since disease development requires the simultaneous presence of a susceptible host, a virulent pathogen and favorable environmental conditions.

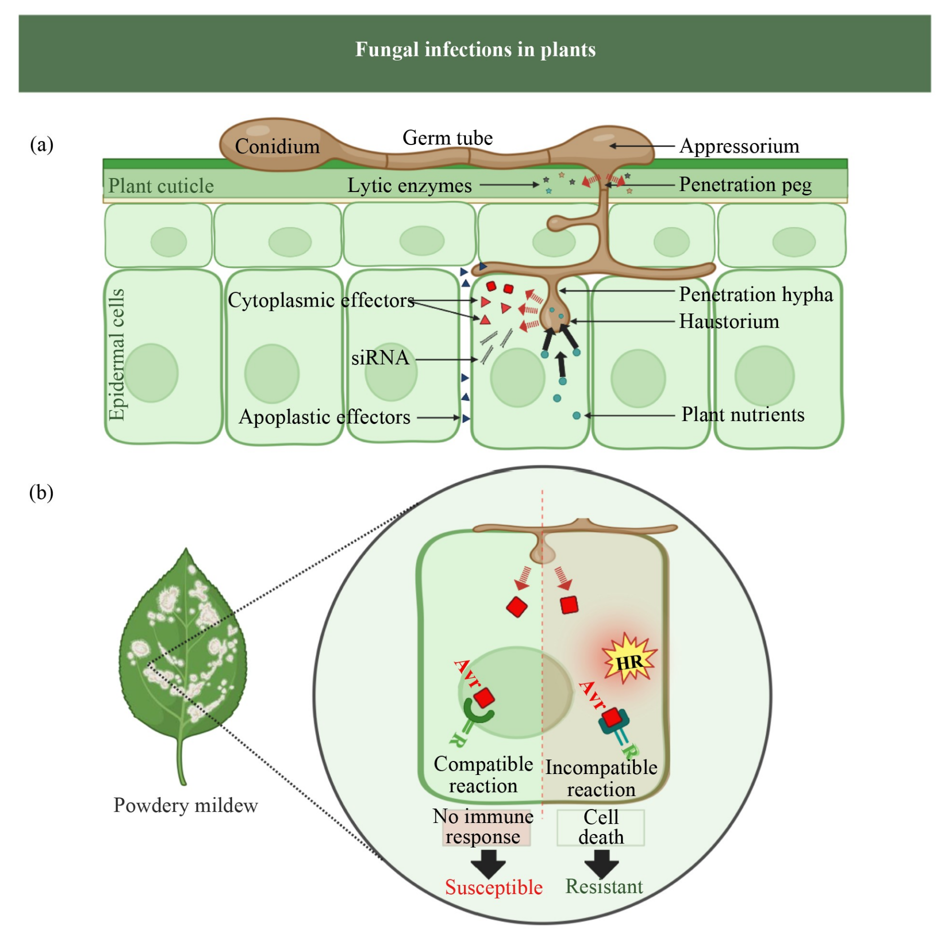


Fig. 1 (a) Fungal pathogen infection process illustrating the formation and function of a melanin-enriched appressorium from the germinating conidium, facilitating penetration of the plant cuticle and cell wall through high turgor pressure and lytic enzymes. The haustorium enters the epidermal cell, where it absorbs plant nutrients and secretes effectors along with small interfering RNA (siRNA), to enhance colonization. (b) Interaction of host resistance (R) proteins with pathogen avirulence effectors determines the immune hypersensitive response (HR) activation, influencing the ability of the pathogen to establish infection. Compatibility or incompatibility in this interaction dictates the outcome of host-pathogen interactions and the incidence of disease. Avr, avirulence.

The interactions between plants and pathogens are dynamic contests of attack and counterattack between the complex defense mechanisms of the plant and invasive strategies of the pathogen as both have evolved genetic components to navigate and counteract each other[43]. The plants first layer of defense are the outer tissues acting as a physical barrier, while the advanced response, known as induced resistance, involves two main forms: systemic acquired resistance (SAR) and induced systemic resistance (ISR), both of which involve several pathways and defense-related compounds that act locally and systemically throughout the plant.

3.1 Systemic acquired resistance

SAR is a slow but long-lasting plant defense response that is activated upon microbial infection or their chemical stimuli, such as chitosan and salicylic acid (SA)[44]. It is initiated upon the recognition of pathogen-associated molecular patterns, microbe-associated molecular patterns, damage-associated molecular patterns or pathogen effector molecules, such as proteins, enzymes, and toxins by pattern recognition receptors present on plant cells. Thus, triggering systemic defense responses such as the production of antimicrobial compounds, reinforcement of cell walls, and the induction of pathogenesis-related (PR) proteins. SAR involves multiple PR genes that control the potential of the plant to activate defenses, however the non-expresser of pathogenesis-related genes 1 has a crucial regulatory role by modulating the expression of PR genes and coordinating the defense response[44,45].

SAR operates through two branches: during pathogen-associated molecular pattern-triggered immunity, a basal defense response that helps plants resist a wide range of pathogens[44]. This is initiated by the recognition of pathogen-associated molecular patterns by pattern recognition receptors and the initiation of a signaling cascade involving mitogen-activated protein kinase. This kinase phosphorylate transcription factors and regulatory proteins, leading to altered gene expression and enhanced defense responses in plants against pathogens[45,46]. During effector-triggered immunity, a rapid defense response that is activated when pathogen effector molecules are detected by nucleotide binding site and leucine-rich repeat protein, leading to a hypersensitive response[45,47]. This response leads to the production and accumulation of reactive oxygen species which can either serve as signaling molecules to amplify defense-related gene expression, reinforce cell wall barriers by lignin and callose deposition, or lead to cell death by oxidative damage to cellular components[44]. The SA pathway is a central component of SAR, with SA acting as the primary signaling molecule that directly contributes to plant defense and activates other metabolites.

3.2 Induced systemic resistance

ISR is a plant defense mechanism that is activated by chemical or biological signals and regulated by a complex hormone signaling networks. It provides a rapid and temporary response both at the site of infection and in unaffected regions[44]. ISR is triggered by beneficial microbes, their byproducts, as well as certain chemicals that stimulate the defense responses, leading to the production of signaling compounds, such as jasmonic acid (JA) and ethylene (ET). Additionally, bacterial volatiles can induce ISR through an ethylene-dependent pathway, while siderophores and cyclic lipopeptide antibiotics can also trigger ISR[48].

JA and ET are key regulators in SA-independent ISR, often stimulated by beneficial soil microbes such as *Bacillus* spp., *Pseudomonas* spp., *Trichoderma* spp. and other rhizobacteria. ISR effectively combats necrotrophic pathogens and insect herbivores sensitive to JA and ET[45]. Unlike SAR, ISR does not rely on the presence of PR and instead primes the immune system of the plant through the expression of JA and ET-responsive genes, leading to faster and enhanced defense responses upon subsequent attacks[49]. Although ISR responses may not directly kill pathogens, it strengthens the overall resistance of the plant to disease by activating systemic defense pathways. Also, beneficial microbe-mediated ISR primarily operates through SA-independent mechanisms. However, some microbial species, such as *Pseudomonas* spp. and *Paenibacillus* spp., can induce SA-dependent ISR, where reactive oxygen species accumulating at the site of colonization act as main elicitors.

3.3 Microbiome-mediated protection

Earlier perspectives portrayed disease incidence as being mainly dictated by plant susceptibility and pathogen virulence. However, current scientific paradigms place more emphasis on crop environment, particularly the plant microbiome which is now considered to be an extension of the plant immune system and a key factor influencing disease outcomes. This microbial ecosystem refers to plant-associated microorganisms that can be found in seeds, on plant surfaces (phyllosphere), inside plant tissues (endosphere), and surrounding the roots (rhizosphere). The composition and activity of these microbial communities can significantly influence crop health and susceptibility to both biotic and abiotic stresses. Among these, rhizospheric communities are crucial for disease suppression, with the presence of certain taxa reducing disease incidence. Soils known to be disease-suppressive often harbor specific microbial groups such communities, such as Actinobacteria, Firmicutes and Proteobacteria. Also, plants are capable of selectively recruiting beneficial microbes during pathogen attacks by releasing root exudates that preferentially enhance microbial chemotaxis, swarming, and biofilm formation, thus promoting their activity in a phenomenon referred to as a cry-for-help[50]. These beneficial microbes mitigate disease through various mechanisms that reduce pathogen growth or metabolic activity, including antimicrobial production, resource competition, and induction of plant immune responses, as previously described. In contrast, disease-conductive soils contain harmful microbes that are either directly pathogenic or can increase disease susceptibility by suppressing plant immune functions. While the plant microbiome in all its forms (endosphere, phyllosphere and rhizosphere) may not always be the primary determinant of diseases, it is critical for modulating disease incidence and severity through dynamic interactions with both the plant host and its pathogens. A greenhouse study on *Pythium aphanidermatum*, the causal agent of tomato root rot, confirmed the ability of two *Streptomyces* spp. isolates obtained from soil to effectively suppress disease incidence and improve overall plant health[51]. These mechanisms and their implications will be discussed in detail in later sections.

4 Disease management strategies

4.1 Plant breeding

Modern plant breeding focuses on enhancing desirable crop traits, such as durable biotic and abiotic stress resistance and high productivity, through molecular techniques, such as marker-assisted selection gene pyramiding and gene editing which in the presence of fully sequenced genomes, to enable the better manipulation of plant genetics[52,53]. Marker-assisted selection-based gene pyramiding allows the efficient selection of multiple R genes or quantitative trait loci that can be stacked to enhance resistance degree and durability[54,55]. For example, pyramiding lines based on different combinations of quantitative trait loci and broad-spectrum R genes resulted in varying resistance level and frequency ($\text{PPL}^{\text{Piz/Pi33}}$ RF = 15.2% and $\text{PPL}^{\text{Pigm/Pi1}}$ RF = 97.7%) to the fungal pathogen, *Magnaporthe oryzae*, causing seedling blast and panicle blast in Mushk Budji rice[55].

Meanwhile, CRISPR/Cas9 systems allow the targeted modification of defense-related genes and the cleavage of viral genomes. Several susceptibility genes have been identified and successfully removed to produce resistant lines against various pathogens. For example, targeting *OsSWEET13* gene enhanced resistance to bacterial pathogen *Xanthomonas oryzae* in *Oryza sativa*, and *DIPM-1*, *DIPM-2* and *DIPM-4* to bacterial pathogen *Erwinia amylovora* in *Malus domestica*[56,57]. Additionally, *CP*, *Rep* and *IR* genes to bean yellow dwarf virus in *Nicotiana benthamiana* and *Arabidopsis thaliana*[58].

4.2 Chemical control

Fungicides combat fungal pathogens through various modes of action classified by the Fungicide Resistance Action Committee, an inter-corporate specialist group that was established in 1981 to provide guidelines for effective fungicide use, resistance management and collaboration with agricultural stakeholders and governmental bodies[59,60]. Generally, preventive fungicides also referred to as contact fungicides remain on the plant surface and directly inhibit or kill fungi and fungal spores. These include copper-based, sulfur-based, phthalimides and other classes, and are considered safer since they can be washed of crop surfaces[61]. Curative fungicides or systemic fungicides are a greater health concern since they can penetrate the surface and move within the plant tissues to control fungal infections. Among the most used are strobilurins, such as azoxystrobin, which inhibit fungal respiration, and sterol biosynthesis inhibitors, which block ergosterol production, a major component of fungal cell membranes[62].

Synthetic fungicides are fast acting and exhibit high effectiveness. For example, strobilurin and triazole application resulted in 95% to 99% and 33% to 65% control of beet rust under greenhouse and field conditions, respectively[63]. Despite their ability to control pests, these chemicals present several health risks. Human serum samples tested for multiple pesticides revealed the presence of several agrochemicals, with fungicides showing the highest prevalence, concentrations, estimated daily intake levels and exposure risks compared to triazine herbicides and neonicotinoid insecticides[64]. In addition, stable chemicals, such as strobilurins, are problematic due to long-term risks of bioaccumulation and biomagnification. The excessive use of agrochemicals has led to the development of several resistant pathogen biotypes, such as *Botrytis cinerea* resistant to benzimidazoles, dicarboximides and fluazinam fungicides[65]. Similarly, *Venturia inaequalis* resistance to benzimidazoles, quinone outside inhibitors and succinate dehydrogenase inhibitors[66]. These findings have driven the search for safer pesticide alternatives.

4.3 Integrated pest management

Integrated pest management (IPM) is a multifaceted approach that focuses on long-term prevention of crop pests by incorporating different strategies, such as cultural practices, resistant cultivars, biological control and forecasting to minimize chemical resistance[67]. IPM promotes natural pest control and minimizes use of disruptive intervention strategies by establishing pest thresholds and economically significant thresholds[68]. Research across nine European countries demonstrated that IPM, supported by decision systems for fungicide applications, effectively helped manage wheat rust diseases, reducing infection rates and fungicide use, while maintaining stable yields with resistant cultivars[69]. Also, IPM is highly adaptable and capable of accommodating new innovations, leading to improvements in yield and quality, and reduction in the use of agrochemicals through the judicious use of synthetic chemicals and the adoption of environmentally safer alternatives, such as microbial inoculants.

4.4 Biological control

The challenges posed by the health and environmental impacts of synthetic pesticides, together with the inherent limitations in plant breeding such as the complexity of trait development and the long time frame involved, have renewed interest in biological control strategies. These methods leverage naturally occurring substances, plant derived products and beneficial organisms to manage plant pathogens with minimal ecological disruption. With the growing urgency for effective and sustainable disease management strategies, beneficial microbial populations have received increasing attention. This is due to their ability to influence plants, plant microbiomes and phytopathogens through direct and indirect mechanisms, ultimately suppressing diseases and improving plant health. Among biocontrol agents, bacterial endophytes are distinctive due to their unique ecological niche within the plant tissues, which allows them to act as both protectors and promoters of plant health. Their close association with the plant host enables them to boost overall crop fitness, prime plant immunity and support resilience to biotic and abiotic stresses. The following sections review the classification, mechanisms and practical applications of biocontrol agents, leading to a more detailed examination of endophytic bacteria as key contributors to disease management and sustainable agriculture.

4.4.1 Definition and classification

Biological control or biocontrol is defined as the direct or indirect reduction or suppression of diseases, causal pathogens or their activity using an antagonistic organism or group of organisms[70,71]. More recent definitions have expanded this concept to include not only the organisms themselves but also their genes, metabolites and natural products with bioactive properties[72]. This broader understanding of biocontrol provides the foundation for biopesticides, which are pest control products derived from living microorganisms or their byproducts. According to the EPA, biopesticides are categorized into three main groups: microbial pesticides, biochemical pesticides and plant-incorporated protectants[73]. Microbial pesticides, comprising nearly 90% of biopesticides products, are commonly based on microorganisms, such as *Bacillus thuringiensis*[74]. Biochemical pesticides include naturally occurring substances (e.g., kaolin clay) and plant-derived substances (e.g., azadirachtin, pyrethrins and nicotine) as well as semiochemicals (e.g., pheromones), which interfere with pest behaviors, such as mating and aggregation. These biopesticides are generally characterized by low toxicity, minimal environmental persistence and negligible crop residues. Lastly, plant-incorporated protectants are pesticidal substances produced by genetically modified crops, through the insertion of pest-resistant genes, such as those encoding *B. thuringiensis* toxins[75].

Biopesticides have gained considerable attention as an alternative to synthetic pesticides due to their diverse and often targeted modes of action, including antifeeding activity, mating disruption, suffocation and desiccation[73]. Their complex mechanisms make them less likely to lead to resistance in pests and pathogens as rapidly as synthetic pesticides. In addition, biopesticides are typically effective at low doses, degrade more rapidly in the environment, and pose lower risks to human health and non-target organisms. Consequently, they are usually exempt from residue tolerance requirements. Also, biopesticides have shown to produce a carbon footprint that is 60% to 90% lower than that of synthetic pesticides, an important advantage given that pesticides and fertilizers contribute significantly to agriculture’s 15% share of global greenhouse gas emissions[25]. These attributes make biopesticides more compatible with food safety standards and sustainable agricultural practices.

For clarity in both scientific and regulatory frameworks, some research groups advocate for clear distinctions, reserving the terms biocontrol agent (BCA) for living organisms (e.g., macrobial and microbial agents) and bioprotectants for non-living substances of biological origin such as microbial metabolites[76]. This review adopts this classification (Fig. 2).

4.4.2 Mechanisms of biocontrol agents

Building on the previous classification, this section considers the primary modes of action by which biocontrol agents exert protective effects against pests. These mechanisms include antagonism, hypovirulence and the induction of host resistance (Fig. 2).

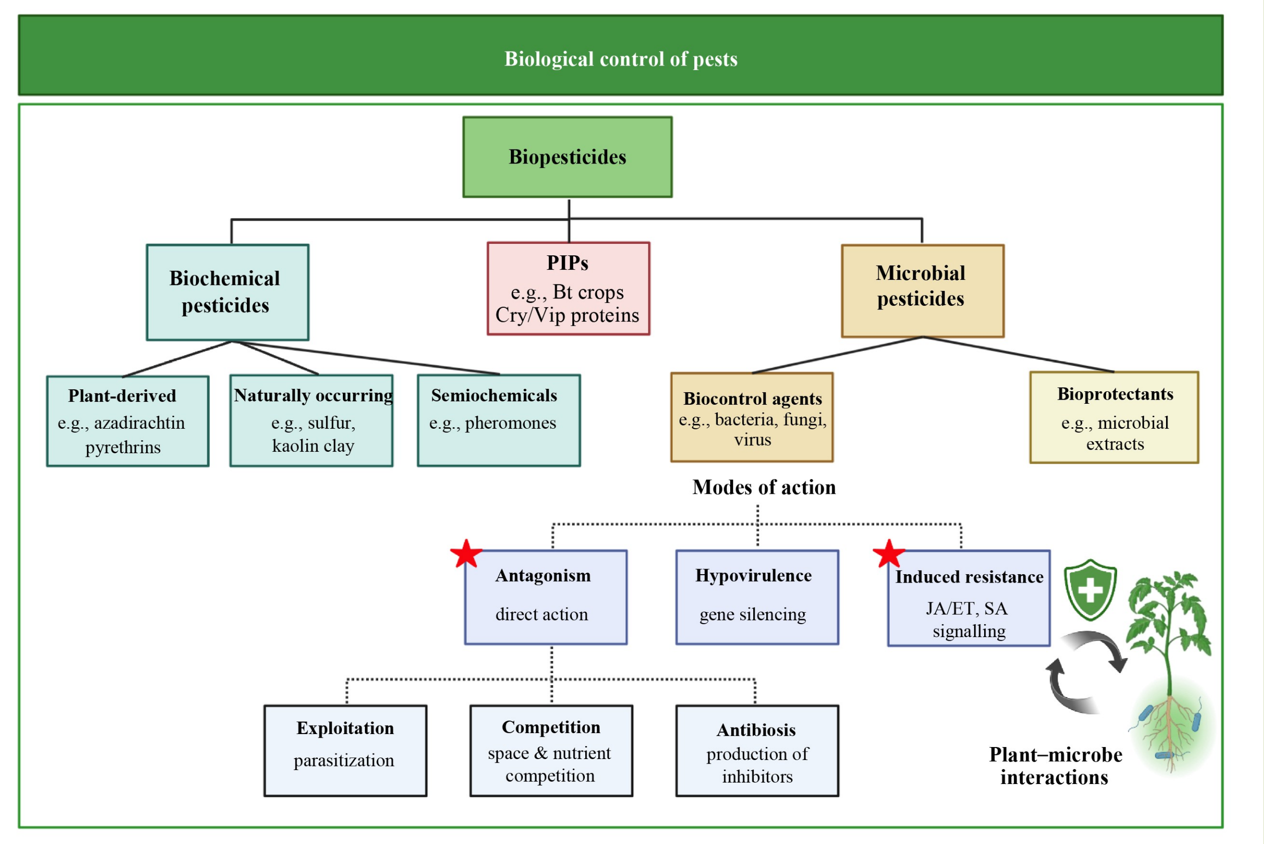


Fig. 2 Classification of biopesticides based on EPA and modes of action of microbial pesticides, highlighting endophytic bacteria (indicated by a red star).

(1) Antagonism

Antagonism involves the direct suppression of pathogens using three main strategies[48]. (a) In exploitation, the BCA directly feeds on the host pest or parasitizes it. For example, *Ampelomyces* parasitizes powdery mildew cells, causing cytoplasm degradation and inhibited sporulation[77]. (b) During competition, the BCA outcompetes the pathogen for space and nutrients, ultimately suppressing through resource depletion. For example, *Pseudomonas fluoroscens* B10 suppresses fusarium wilt by releasing siderophore pseudobactin which sequesters rhizospheric iron, an essential nutrient for fungal colonization and pathogenicity[78]. (c) Antibiosis refers to the production inhibitory compounds or toxins by the BCA. Examples include agrocin 84, produced by *Agrobacterium* to control *Agrobacterium tumefaciens*, the causal agent of crown gall[79]. Also, hydrogen cyanide produced by *Pseudomonas fluoroscens* strain PF1 to control *Macrophomina phaseolina*, a causal agent of rot disease in many crops[80]. Other reported antibiotic compounds include bacillomycin D, iturin A and mycosubtilin produced by *B. subtilis*, and 2,4-diacetylphloroglucinol and phenazines produced by *P. fluorescens*[81–83].

(2) Hypovirulence

This mechanism refers to the reduction in pathogenicity, viability or reproduction of a virulent fungal strains following the introduction of a weakened and less virulent strain acting as a BCA[84]. Hypovirulent strains typically carry double-stranded RNA mycoviruses that induce gene silencing through RNA interference, which involves the degradation of specific mRNA sequences. This effectively suppresses the expression of pathogenesis-related genes, ultimately reducing the virulence of the fungal pathogen[85,86]. For example, *Hypovirus FGHV2*, which infects *Fusarium graminearum*, was shown to significantly reduce both the mycelial growth rate and the synthesis of deoxynivalenol, a harmful mycotoxin produced by the pathogen[87].

(3) Induction of host resistance

As previously discussed, this mechanism involves the activation of the host plant defenses to enhance its ability to resist pathogenic attacks. The process is initiated by the release of chemical elicitors by the BCAs, which are then perceived by the host, leading to the activation of defense-related signaling pathways, such as the JA/ET or SA pathways[88,89]. Certain root-colonizing microbes, such as *Pseudomonas* spp. and *Trichoderma* spp., along with various plant growth-promoting rhizobacteria (PGPR), have been documented as potential elicitors of host resistance[90,91]. For example, *Pseudomonas chlororaphis* subsp. *aurantiaca* (syn. *Pseudomonas aurantiaca*) ST-TJ4 emits volatile organic compounds (VOCs) that trigger systemic resistance to *Verticillium dahliae*, the causal agent of Verticillium wilt in cotton. This response involves the activation of SA and hydrogen peroxide signaling pathways in the host, leading to the accumulation of resistance-associated proteins (e.g., chitinases) which degrade fungal cell walls, as well as secondary metabolites (e.g., flavonoids and phenols) that exhibit antimicrobial and antioxidant activity[92].

4.4.3 Common biocontrol agents

The implementation of BCAs in disease suppression can involve a variety of species. Prominent biocontrol agents are in the bacterial genera *Bacillus*, *Lysobacter, Pantoea, Pseudomonas* and *Streptomyces*, as well as fungal genera, such as *Aspergillus*, *Gliocladium*, *Petriella*, *Trichoderma* and non-pathogenic *Fusarium* spp.[93,94]. Some of these biocontrol agents, including bacteria, such as *Pseudomonas chlororaphis,* and fungi, such as *Ampelomyces quisqualis*, *Trichoderma polysporum* and *Verticillium lecanii*, have already been commercialized[95].

For fungal diseases control, several documented cases have shown successful control using BCAs that are comparable to synthetic fungicides. For example, in a two-year field study conducted on three strawberry cultivars, *Trichoderma atroviride* LU132 gave significant suppression of *B. cinerea* sporulation on leaves and flowers comparable to the fungicide control fenhexamid[96]. In a recent study, the volatile compounds and the lipopeptides extracted from *Bacillus subtilis* CTXW 7-6-2 effectively inhibited the growth of *Rhizoctonia solani* in tobacco. Also, treated seedlings showed improved growth parameters and upregulation of diseases resistance genes[97]. Another study revealed that *B. subtilis* JNF2 successfully suppressed the soilborne pathogen *Fusarium oxysporum* on cucumber seedlings, surpassing the efficacy of the synthetic fungicide hymexazol, and promoted seedling growth through the production of antimicrobial compounds, hydrolytic enzymes, siderophores, and indoles[98]. Similarly, *Pseudomonas rhodesiae* HAI-0804 conferred protection against damping off and root rot induced by *Globisporangium ultimum* (syn. *Pythium ultimum*) in cucumber, with enhanced biocontrol linked to glutamate stimulated siderophore production, root colonization and biofilm formation despite the absence of direct antibiotic activity[99].

5 Plant microbiome and beneficial bacteria

5.1 Recruitment of microbiota

Plant ecosystems and soils provide diverse environmental conditions that support the growth and development of a wide range of plant-associated microbial communities. High populations densities are primarily found in rhizospheric soils, where root exudates serve as a major source of organic carbon, making these areas aggregations for microbial activity[100]. As result, microorganisms can establish pathogenic, neutral or beneficial relationships with the host. The plant microbiome is a product of plant-microbe coevolution and adaptation, which is further shaped through the dynamic processes of microbial filtering and recruiting[101,102]. Within the plant microbiome, the consistent presence of certain core microorganisms, such as *Agrobacterium*, *Fusarium* and *Pseudomonas*, in the rhizosphere, indicates preferential recruitment and adaptation to coexist with the host and participate in its functions[103,104]. Consequently, identifying these microorganisms and understanding their behavior within plant systems is beneficial for research aimed at leveraging beneficial microbial communities, particularly since many of these induce beneficial effects on growth, productivity and pathogen resistance.

5.2 Bacterial endophytes

According to Omomowo and Babalola[105], endophytes are microbial communities that inhabit the internal tissues of host plants without causing symptoms. These communities competently colonize various plant tissues and organs including roots, stems, leaves, flowers, fruits and seeds, with the highest densities typically found in roots, followed by stems and leaves[106,107]. Their population density and distribution are influenced by factors, such as host plant variety, health and developmental stage, isolation procedures, environmental factors, soil pH, temperature and the presence of pathogens. Once established, beneficial endophytic bacteria can reside in the host plant for a part or the entirety of their life cycle, during which they can interact with the host plant both directly and indirectly, engaging in essential roles in plant systems (Fig. 2)[108].

The ability of endophytes to colonize internal tissues and organs, and establish beneficial relationships makes them particularly advantageous since they remain protected throughout their life cycle from external stresses[109,110]. Notably, the beneficial effects of endophytes are not limited to their original plant hosts. Several studies have demonstrated that both native and non-native endophytes can be successfully introduced into different crops, where they confer protective and growth-promoting effects. For example, inoculating Indian long pepper (*Piper longum*) with native endophytic bacteria *Actinobacter soli* PlS14 and *Enterobacter hormaechei PlR15* increased root percentage by 50% in cuttings and promoted growth in plants[111]. Meanwhile, the inoculating cucumber seedlings in a hydroponics system with the non-native *Pseudomonas* sp. ALR1619 provided short- to medium-term protection against *Pythium* blight, increasing survivability by 41% when the pathogen was introduced 1 day after inoculation and by 38% when introduced after 5 days, compared to the control[112].

In addition to their roles in biocontrol, many bacterial endophytes also exhibit plant growth-promoting traits that position them as effective crop biostimulants. According to the EU Regulation 2019/1009, a plant biostimulant is defined as “a product stimulating plant nutrition processes independently of the product’s nutrient content with the sole aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: (a) nutrient use efficiency; (b) tolerance to abiotic stress; (c) quality traits; (d) availability of confined nutrients in soil or rhizosphere”[113,114]. Many bacterial endophytes fulfill these criteria through mechanisms that enhance nutrient availability and uptake, modulate plant hormone levels or improve stress resilience.

5.2.1 Direct effects

(1) Nitrogen fixation

Nitrogen is a primary plant nutrient, being essential for development and a fundamental component in amino acids, proteins, nucleic acids and chlorophyll, contributing significantly to structural integrity and essential functions, such as photosynthesis. Despite its atmospheric abundance as a gas, it is only available for plant uptake in its reduced form, ammonia[115,116]. However, nitrogen fixers can induce the formation of symbiotic root structures termed nodules on host roots that fix atmospheric nitrogen using nitrogenase enzyme, ultimately leading to the production of ammonia (Fig. 3)[115,117]. The molecular mechanisms leading to this symbiotic relationship can be divided into two stages, nodule formation and invasion, followed by the establishment of symbiotic nitrogen fixation within nodule cells. Also, rhizobia possess the MoFe-containing variant of the nitrogenase enzyme system, enabling them to fix nitrogen[118]. Despite the aerobic nature of rhizobia, the nitrogenase enzyme is highly susceptible to oxygen. To circumvent this, rhizobia induce the formation of nodules, specialized organs characterized by an extremely low-oxygen environment. Within these nodules, the synthesis of leghemoglobin aids in oxygen diffusion to bacteroids, allowing nitrogenase to function effectively[118]. Numerous nitrogen-fixing bacteria, including *Achromobacter*, *Azoarcus*, *Azorhizobium*, *Burkholderia*, *Frankia*, *Herbaspirillum* and *Rhizobium*, have been recognized[119,120].

(2) Phosphate-solubilization

Phosphorus is the second most important nutrient for plant growth. Its availability to plants is severely limited due to its presence in insoluble forms in the soil. Plants can only assimilate phosphorus in the form of monobasic or dibasic phosphates[120]. Phosphate-solubilizing bacteria facilitate the availability of phosphate, thereby enabling plants to assimilate it effectively (Fig. 3)[121]. The solubilization of organic phosphates uses enzymes, such as phytases, carbon-phosphorus lyases and phosphatases[122]. Meanwhile, inorganic phosphate solubilization is done mainly through the production of organic acids which chelate cations and reduce surrounding soil pH, allowing the release of phosphates[123,124]. Documented effective PSM belong to the genera *Bacillus*, *Pseudomonas* and *Rhizobium* along with non-symbiotic nitrogen-fixing organisms, such as *Azospirillum* and *Azotobacter*[125,126].

(3) Indole-3-acetic acid production

Indole-3-acetic acid, an auxin-type hormone, is vital for cell division, elongation and tissue differentiation. IAA is crucial for nutrient uptake, root developmen, and biomass

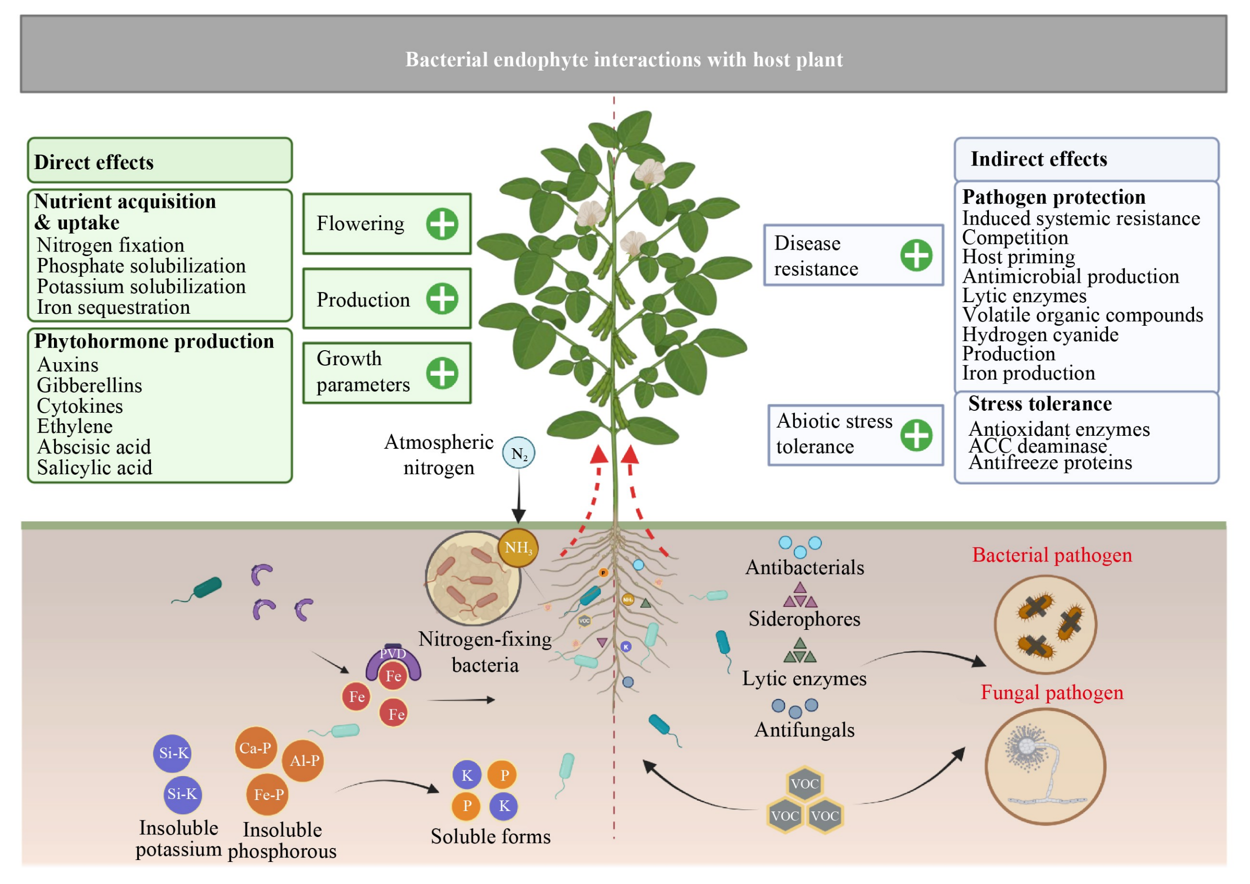


Fig. 3 Diagram illustrating the primary direct and indirect activities of plant growth-promoting bacterial endophytes, including enhanced pathogen protection, stress tolerance, nutrient acquisition and uptake and phytohormone production.

increase[127,128]. IAA production is recognized as an effective indicator for identifying beneficial microbes with plant growth promotion capabilities[120,129]. Tryptophan, a natural root exudate, serves as the primary precursor for IAA biosynthesis. Multiple pathways, such as indole-3-acetamide, indole-3-pyruvate, tryptamine, tryptophan side-chain oxidase and tryptophan-independent pathways, use tryptophan for IAA synthesis[120,130]. IAA production contributes to plant-bacteria communications and influences root nodulation and plant stress responses[131]. Additionally, endophytes exhibiting high IAA production can influence transcriptional variations leading to higher nitrogenase activity in plants[120,132]. Endophytic bacteria, such as *B. subtilis*, *B. aryabhattai*, *Klebsiella pneumoniae*, *Microbacterium trichotecenolyticum* and *Paenibacillus kribbensis*, were found to be IAA producers[133].

(4) 1-Aminocyclopropane-1-carboxylate deaminase

Ethylene is crucial for regulating cell development, overall plant growth, and aiding in stress response[115,134]. When ethylene surpasses its threshold in plant tissues due to increased activity of the ACC oxidase enzyme, it leads to stress ethylene, impacting root and shoot development. Also, ethylene is primarily derived from the conversion of S-adenosyl methionine by ACC synthase, with 1-aminocyclopropane-1-carboxylate (ACC) serving as the main precursor. In stressful situations, heightened ACC synthase activity leads to an increased production of ethylene[120,128]. The existence of ACC deaminase producing PGPRs in the rhizospheric soil of stressed plants aids in alleviating this condition by degrading ACC, leading to a reduction in ethylene levels and promoting the restoration of normal plant development and root elongation[120,135].

5.2.2 Indirect effects

(1) Siderophore production

Iron is an essential micronutrient crucial for photosynthesis and as acts as a cofactor in chlorophyll synthesis. However, despite its abundance in nature as Fe^{3+}, this form cannot be absorbed by plants. However, certain PGPRs release siderophores such as pyoverdine with a high affinity for rhizospheric iron (Fe^{3+}), subsequently chelating it and converting it to an absorbable form (Fe^{2+}) (Fig. 3)[120,136]. Additionally, siderophore-producing PGPBs create an iron-limiting environment, impeding pathogen growth and reducing pathogenicity by sequestering rhizospheric iron. This dual action benefits plant health and limits pathogenic threats. Siderophores have been consistently reported to be produced by *Pseudomonas* spp. and *Bacillus* spp.[137,138].

(2) Hydrogen cyanide production

Certain PGPRs produce hydrogen cyanide, and while the low levels of HCN alone may not be highly effective, these bacteria often combine HCN production with the synthesis of antibiotics or cell wall degrading enzymes[115,139]. This synergism with HCN enhances the efficacy of antifungals against fungal pathogens and prevents the development of resistance. HCN producing genera include *Aeromonas, Alcaligenes, Bacillus, Pseudomonas* and *Rhizobium*[140,141].

(3) Antibiotic production

PGPRs primarily counteract the harmful effects of phytopathogens by synthesizing antibiotics (Fig. 3). Antibiotic efficacy in controlling a particular pathogen may not necessarily apply to other pathogens on the same plant, and the behavior of the PGPR can vary under diverse field conditions. Bacteria from the genera *Bacillus* and *Pseudomonas* have been prolific sources of antibiotics with applications including antifungal, antibacterial, antiviral, phytotoxic, antioxidant and cytotoxic properties. Numerous antibiotics with diverse applications have been derived from these genera. Examples from *Pseudomonas* spp. include ecomycins, 2,4-diacetyl phloroglucinol, pseudomonic acid, phenazine-1-carboxylic acid, azomycin, kanosamine and karalicin. Similarly, *Bacillus* spp. contribute antibiotics such as bacilysin, fengycin, iturin, subtilin, subtilosin, surfactin and Tas A[115,142]. In addition, endophytes produce a variety of natural products, such as steroids, terpenoids, flavonoids and alkaloids, which are used as antibiotics, biological control agents and anticancer agents, and various other bioactive compounds[143].

(4) Cell wall degrading enzymes production

PGPR can produce a variety of extracellular hydrolytic enzymes, which have been widely reported for their roles in controlling plant pathogens[144]. These enzymes include a diverse group of compounds, most notably glycoside hydrolases (e.g., β-1,3-glucanase, chitinase and cellulase), peptidases (e.g., proteases) and oxidoreductases (e.g., catalase), among others[145]. They function by degrading essential components of phytopathogen cell walls and membranes, including chitin, cellulose, hemicellulose, proteins and even DNA[146]. When paired with antimicrobial metabolites, these enzymatic activities enhance their biocontrol potential, making them particularly effective against fungal spores and mycelia. Thus, PGPR act as potent extensions of the host plant defense mechanisms (Fig. 3). Beyond their role in pathogen suppression and control, hydrolytic enzymes also facilitate the colonization of plant roots by PGPR[120,147]. Endophytic bacteria from various genera, including *Azotobacter*, *Bacillus*, *Cladosporium*, *Enterobacter*, *Pseudomonas*, *Rhizobium*, *Serratia* and *Streptomyces*, have been reported to secrete hydrolytic enzymes that exhibit biocontrol activity against important fungal pathogens such as *F. oxysporum* and *R. solani,* positioning them as promising tools for biocontrol[120,148,149].

(5) Volatile organic compound production

VOCs serve as signaling molecules for cellular communication and contribute to restricting the growth of pathogens (Fig. 3)[120,150]. To date, 346 distinct VOCs have been identified from species, such as *Bacillus*, *Pseudomonas*, *Erwinia* and *Staphylococcus*[151]. *Bacillus* endophytes, such as *B. subtilis*, have biocontrol activity by directly protecting plants against phytopathogens or indirectly inducing plant resistance. For example, *B. subtilis* strain DZSY21 inhibits the growth of the fungal pathogen *Curvularia lunata*[152], while VOCs from *Bacillus velezensis* strain ZSY-1 have strong antifungal activity against *Alternaria solani* and *B. cinerea*[150,153]. In addition, VOCs emitted by *Bacillus* spp. can modify root architecture and stimulate plant growth parameters[154].

(6) Quorum sensing

Quorum sensing (QS) is a bacterial communication process involving the production, detection and response to extracellular signaling molecules known as autoinducers. These allow cooperation or interference (quorum quenching) between different bacterial taxa. As bacterial population density increases, autoinducers accumulate, enabling collective alterations in gene expression and controlling diverse physiologic functions such as bioluminescence, sporulation, antibiotic production, biofilm formation and virulence factor secretion[155,156]. In addition, QS alters several activities such as symbiosis, competence, conjugation and motility[157]. In general, gram-negative bacteria communicate using small molecules, such as acyl-homoserine lactones, whereas gram-positive bacteria use oligo-peptides, called autoinducing peptides[155,158], both are crucial for bacterial gene regulation at high cell density, orchestrating complex interactions within plant microbiomes. HSLs perceived by plants can influence metabolism, immune response and root development. For example, the endophyte M6 swarms toward *F. graminearum*, forming a barrier and killing the pathogen. Studies have shown that plant-associated microbiomes are enriched with HSL, with 40% to 50% of bacteria having HSL activity[101,159]. This high prevalence highlights the potential role of AHL-mediated communication in coordinating microbial interactions within the plant environment.

Recent studies have shown that QS in *B. subtilis* shapes the fungal microbiome across citrus plant compartments, where quorum quenching mutants enrich pathogenic fungi and the wild type promote beneficial taxa, such as *Trichoderma*. Hence, highlighting the role of bacterial QS in microbiome homeostasis and disease suppression[160]. Similarly, endophytic *B. subtilis* EBS9 from *Tecomella undulata* exhibited quorum quenching activity via diketopiperazine production, disrupting QS in *Pectobacterium carotovorum* and significantly reducing its virulence. This interference also led to improved plant growth parameters both *in vitro* and *in vivo* experiments, highlighting its potential as in effective biocontrol and biostimulant[161].

While not classified as autoinducers, terpenes can modulate QS through their quorum quenching activity or antimicrobial properties, thereby indirectly influencing microbial population dynamics. Terpenes fulfill diverse ecological functions, including eliciting plant responses, such as carotenoid biosynthesis, and acting as chemical defenses against herbivores and pathogens[162]. Notably, genes involved in terpene biosynthesis are highly represented in among plant-associated bacteria, with 49% of strains carrying a gene encoding terpene synthase, indicating a possible role in plant-microbe interactions[101,159].

6 Challenges of microbial formulations

Microbial formulations are increasingly recognized as efficient, eco-friendly and sustainable alternatives to the more widely-used agricultural inputs, such as pesticides and fertilizers. However, their adoption in large-scale agriculture remains limited due to several technical, biological and market-related challenges. Although generally considered low in toxicity and environmental impact, microbial pesticides face strong competition from synthetic pesticides, which are easier to produce, possess longer shelf-life and benefit from well-established industrial production systems[163]. Consequently, synthetic pesticides tend to be significantly less expensive and readily available in global markets[164].

A major limitation of microbial pesticides is their field instability and their generally narrow spectrum of activity. In contrast, synthetic pesticides are stable and can be used to control multiple pests with their broad activity. Also, while laboratory trials and early-stage testing are typically conducted under controlled conditions, field testing introduces several unaccounted variables[165]. Thus, field performance can vary significantly, often requiring multiple applications and careful considerations based on crop, pest and environmental conditions, such as soil type, pH and temperature, to optimize performance[166]. Additionally, microbial pesticides typically exhibit slower modes of action and reduced efficacy under high pest pressure, making them more effective as preventive measures or when pest populations are at low levels[167].

Additional constraints include challenges related to dosage optimization, application timing, compatibility with existing agrochemicals or production practices, and field persistence, the effects of which remain poorly understood. Also, the potential for resistance development, lack of farmer awareness, and inadequate regulatory frameworks such as the absence of standardized quality control measures, impede their broader adoption. From a scale-up standpoint, microbial formulation are also hindered by production-related challenges such as batch-to-batch variation, risks of contamination or strain mutation, waste management issues (especially in fermentation-based formulations), and the complexity of downstream processing required for metabolite purification[168].

Similar limitations affect microbial endophytes, which are being investigated not only for their biocontrol potential, but also for their broader roles in promoting plant growth, enhancing disease resistance and improving abiotic stress tolerance. Despite their promise, the most effective strategies for integrating endophytes in agricultural systems remain uncertain. Common application methods such as soil inoculation, foliar spraying and seed dressing, produce varying results under field conditions. Additional key obstacles include the lack of vertical transmission necessitating repeated introduction, and the unpredictability of interactions within complex soil microbiomes and the presence of pollutants that may interfere with endophyte establishment and success[169,170].

Although some studies indicate that reduced input rates of agrochemicals may enhance beneficial interactions with endophytes, successful field implementation will require deeper insights into their life cycles, genome plasticity and potential latent pathogenicity[169,171]. As with microbial pesticides, improving the consistency, predictability and robustness of endophyte performance is essential to ensure their establishment as dependable agricultural tools. This will necessitate further research especially in areas of endophyte-host and soil microbiome interactions as well as rigorous biosafety evaluations, including assessments of toxins production[169].

The address several obstacles limiting large-scale field adoption, the development of effective and stable microbial formulations is critical. These must retain their properties throughout storage, transportation and field application. Emerging technologies, such as nanotechnology, offer promising solutions by enhancing delivery efficiency, improving stability of active compounds and enabling controlled release. Nanotechnology-based formulations can reduce application rates, minimize off-target effects and environmental contamination and lower worker exposure, contributing to safer and more sustainable pest and crop management[172,173].

7 Nanotechnology in agriculture

Nanotechnology is the discipline that encompasses the synthesis and applications of particles spanning between 1 and 100 nm[174]. Consequently, they are smaller in size than bacteria, bacteriophages and viruses. Nanoscale materials have distinct properties that diverge from those of their macroscopic equivalents. In their reduced form, nanoparticles can be used in several applications due to their increased surface-to-volume ratio, reactivity and possible biochemical activity[175]. Due to their unique properties, nanotechnology finds diverse applications in agriculture, including nanofertilizers and nanopesticides.

7.1 Nanofertilizers

Nanofertilizers encompass nanomaterials that either serve as nutrients or function as carriers or additives for the nutrients[176]. Several types of nanofertilizers have been developed, incorporating nanoparticles, including carbon nanotubes, iron, molybdenum, silica, silver, titanium and zinc[177]. The application of nanofertilizers has demonstrated beneficial effects on seed germination, root and shoot elongation, plant biomass and chlorophyll concentration in treated crops[178,179]. Nanofertilizers have enhanced mobility in their colloidal suspension state due to increased entropy, thereby enabling more efficient penetration of plant cell membranes compared to standard fertilizers[180]. In addition, nanofertilizers minimize the losses of mobile nutrients, create slow-release fertilizers and enhance the accessibility of poorly available nutrients[181].

7.2 Nanopesticides

The application of nanotechnology in plant protection encompasses the usage of metal nanoparticles, nano-encapsulated active substances and nanocomposites[182]. Additionally, nanomaterials that show potential for improving pesticide effectiveness include fibers, gels, nanoemulsions and vesicles[183]. Nanomaterials, including nanosilver, nanocopper, nanosilica and nanoformulations of synthetic pesticides, have efficacy against diverse insect pests and fungal pathogens[184]. Silver nanoparticles have extensive antifungal efficacy against various plant pathogens, including *Alternaria* spp., *Fusarium* spp. and *Rhizoctonia* spp.[185]. They can impede mycelial growth, spore germination, and compromise fungal cell membranes. Nanoformulations improve solubility, enhance their efficacy and reduce environmental impact, prolong shelf-life, and facilitate release, while the incorporation of essential oils and plant extracts further extends shelf-life without adversely affecting non-target organisms[186]. Nanoemulsions with diminished surfactant concentrations enhance the retention and absorption of active ingredients by plants, facilitating efficient targeted delivery while reducing effects on non-target organisms[187].

7.3 Applications for microbial agents

Microbial agents in the field are highly susceptible to degradation and diminished efficacy due to numerous biotic and abiotic factors, such as UV radiation, temperatures extremes and soil pH variations. To mitigate these effects, different nanotechnologies are being actively investigated to address issues such as stability, release profile and bioavailability.

7.3.1 Encapsulation

Microencapsulation and nanoencapsulation serve as mechanisms to address these challenges while simultaneously improving efficiency, commercial feasibility, formulation stability and minimizing losses due to volatility[188]. Throughout this process, bioactive compounds are encapsulated by a carrier material, leading to the creation of particles or capsules at the micrometer or nanometer scale[189]. The encapsulated substances, termed the core, fill or internal phase, are protected by the coating materials (carrier material), known as wall material, membrane, capsule, shell, matrix or external phase[190]. In the final product, this encapsulation contributes to the improvement of bioavailability, controlled release and precision in targeting bioactive compounds[189].

The selection of an appropriate encapsulating agent is essential for the success of the encapsulation process. In food and agriculture applications, the selected wall material must be deemed safe, function efficiently as an emulsifier, retain low viscosity at elevated concentrations, and have advantageous dissolution and network-forming characteristics[191]. Also, it must maintain stability amidst environmental fluctuations and prevent cross-reactivity with bioactive compounds.

For example, the encapsulation of *Pseudomonas* spp. using alginate beads enriched with SA and zinc oxide nanoparticles further improved its IAA production as well as its antifungal activity[192]. In another study, the encapsulation of *B. subtilis* CC-pg104 alginate enriched with humic acid resulted in increased viability and improved release even at different pH levels[193]. Also, the encapsulation of savory essential oil with Arabic gum gelatin improved its suppressive ability as a herbicide[194]. In a recent study, the encapsulation of *B. subtilis* in chitosan gel beads prolonged its viability for up to 90 and 180 days while maintaining its antifungal activity against *Fusarium avenaceum* and *R. solani*[195]. Similarly, the encapsulation of *Bacillus megaterium* in a poly(vinyl alcohol)-cationic starch-zinc oxide matrix via spray drying enhanced protection under extreme field-like conditions. Encapsulated cells retained viability after prolonged exposure to high temperatures, UV radiation and pesticide treatment. The formulation doubled the shelf-life to 14 months. Greenhouse application led to increased crop biomass and improved P and Zn uptake[196]. Likewise, the microencapsulation of *B. velezensis* BV9 with alginate-zedo gum improved cell viability, release profile, stability and resulted in complete suppression of *Gaeumannomyces graminis* var. *tritici* in wheat greenhouse experiments[197].

These, in addition to other polymers, such as chitosan, pectin, shellac and starch, hold promise as encapsulating compounds with potential use in agricultural production, such as biofertilizers, biopesticides and seed treatment agents (Fig. 4(a))[191].

7.3.2 Pickering emulsion

This refers to emulsions that are stabilized in two immiscible liquids using solid nanoparticles. Thus, stabilizing the system by reducing the interfacial energy[198]. Pickering emulsions have been gaining attention for their advantages in cost, quality, and sustainability. Also, due to their ability to stabilize particles and their high loading capacity makes them attractive for many applications[199].

Nanoemulsions can be used to give superior pesticide delivery systems characterized by enhanced kinetic stability, smaller size, low viscosity and optical transparency[200]. Also, both nano-emulsions and microemulsions can improve the solubility and bioavailability of active ingredients.

Also, inverse Pickering emulsion (water-in-mineral oil emulsion), which consists of dispersed droplets of water stabilized in oil is effective in stabilizing live bacterial cells[201]. This encapsulation mechanism holds promise as it can also be used to carry water soluble components of bacteria (Fig. 4(b)). In one study, *B. thuringiensis serovar aizawai* cells, spores and crystals were encapsulated in water droplets and stabilized by hydrophobic silica nanoparticles. This resulted in improved pesticidal activity as compared to controls of these materials in water suspension[202]. A more recent study has shown that the encapsulation of *B. subtilis* and *Bacillus amyloquefaciens* in nanosilica-based inverse Pickering emulsion enhanced their antiviral activity against groundnut bud necrosis orthotospovirus in tomato and chickpea. The formulation significantly reduced lesions, virus titer by threefold and overall disease by about 78% in tomatoes[203].

7.3.3 Centrifugal spinning

Centrifugal spinning, a widely used nanofiber production method in the food industry, applies centrifugal force to create nanofibers. In a study by Campaña and Arias[204], polyethylene oxide nanofibers were used as a delivery system for arbuscular mycorrhizal fungi by coating nanofibers of common bean seeds. The centrifugal spinning technique proved highly effective in producing continuous and uniform polyethylene oxide nanofibers, facilitating the creation of a fibrous mat for the application of the mycorrhizal inoculant. Additionally, the nanofibers were found to be successful in fixing the inoculant between fiber sheets and on their surfaces (Fig. 4(c)). Thus, polyethylene oxide nanofibers were found to be particularly successful as a carrier for a mycorrhizal fungal inoculant, preserving both infective capacity and beneficial properties without adverse effects[204]. A recent study embedded *B. subtilis* onto poly (3-hydroxybutyrate) fibers using simultaneous electrospinning and electrospraying with chitooligosaccharide. This resulting biohybrid material exhibited improved wettability, mechanical properties, supported bacterial proliferation and allowed effective inhibition of *Alternaria* spp. and *Fusarium* spp.[205].

8 Prospects and conclusions

The earlier description of endophytes as per the first definition, focuses exclusively on culturable endophytes, which represents a very small fraction of the total endophytic community. As a result, most plant-endophytic interactions remain inadequately investigated. However, recent advances in sequencing and bioinformatic technologies, now allow for the comprehensive analysis of entire endophytic consortia, including unculturable taxa. This is particularly relevant for medicinal crops with poorly researched endophytic communities, such as *Cannabis sativa*, as investigation had been previously limited due to legal and regulatory barriers. Examining the endophytic communities of medicinal crops remains a promising field, especially for biocontrol purposes. For example, bacterial

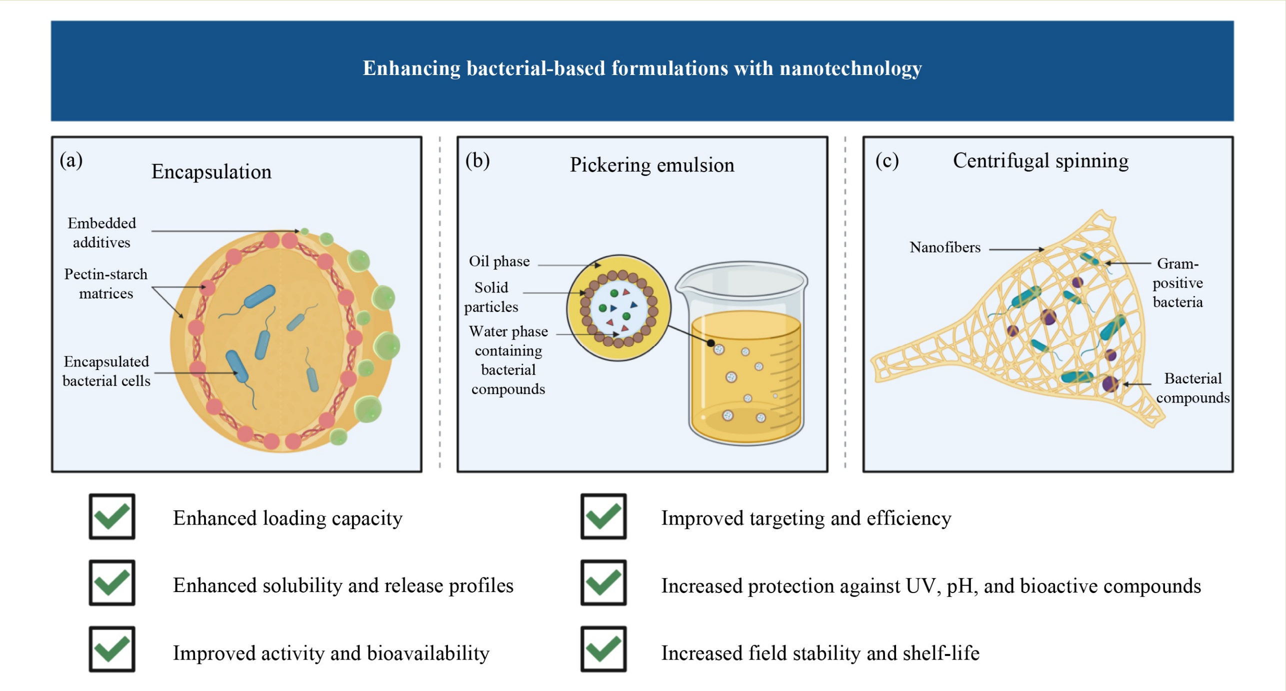


Fig. 4 Schematic representation illustrating various nanotechnology applications, such as (a) encapsulation, (b) Pickering emulsion and (c) centrifugal spinning, used to enhance the stability and efficacy of bacterial-based formulations.

endophytes in cannabis plants exhibit significant chemodiversity, positioning them as promising candidates for disease biocontrol. Similarly, *Chelidonium majus*, a medicinal plant known for its pharmaceutical properties, offers another compelling case. However, research on *C. majus* has primarily focused on its extract, leaving its endophytic communities and biochemical profiles largely unexamined.

The rising demand for sustainable agricultural inputs has driven rapid growth in biopesticide market, positioning bacterial endophytes as timely and promising tools. They have demonstrated the ability to enhance plant growth, suppress pathogens and mitigate abiotic stress, indicating a role in transitioning global agriculture toward greater resilience and sustainability. However, translating these capabilities into wider field-scale success will require addressing several persistent scientific, technical and regulatory challenges.

Scaling microbial inoculants remains constrained by formulation instability, short shelf-life and inconsistent field performance across environments. Also, the use of non-native strains raises concerns around microbiome disruption, ecological imbalance and potential toxin production, which remain insufficiently studied and poorly regulated. Rather than treating microbial products as simple replacements to for synthetic agrochemicals, future research should focus on integrating them into broader regenerative systems. This includes soil health management, crop rotation and cultural control, supported by evaluation frameworks that are tailored to the dynamic nature of microbial agents rather than those designed for synthetic chemical inputs. Long-term ecological outcomes and field-based system integration should become central evaluation criteria.

Further progress also hinges on innovation in formulation technology. Technical limitations, including desiccation, UV sensitivity and viability loss, must be addressed to ensure reliable field performance. While short-term metrics, such as efficacy and availability, remain important, long-term advantages of microbial products will be reduced risk of resistance development, synergy with the host and soil microbiome, lower environmental impact, compatibility with IPM strategies and alignment with regenerative and sustainable agricultural practices. These factors are illustrated in Fig. 5.

Emerging technologies offer promising tools to overcome many of the field-related challenges. Nanotechnology, for example, may enhance microbial delivery systems, improve

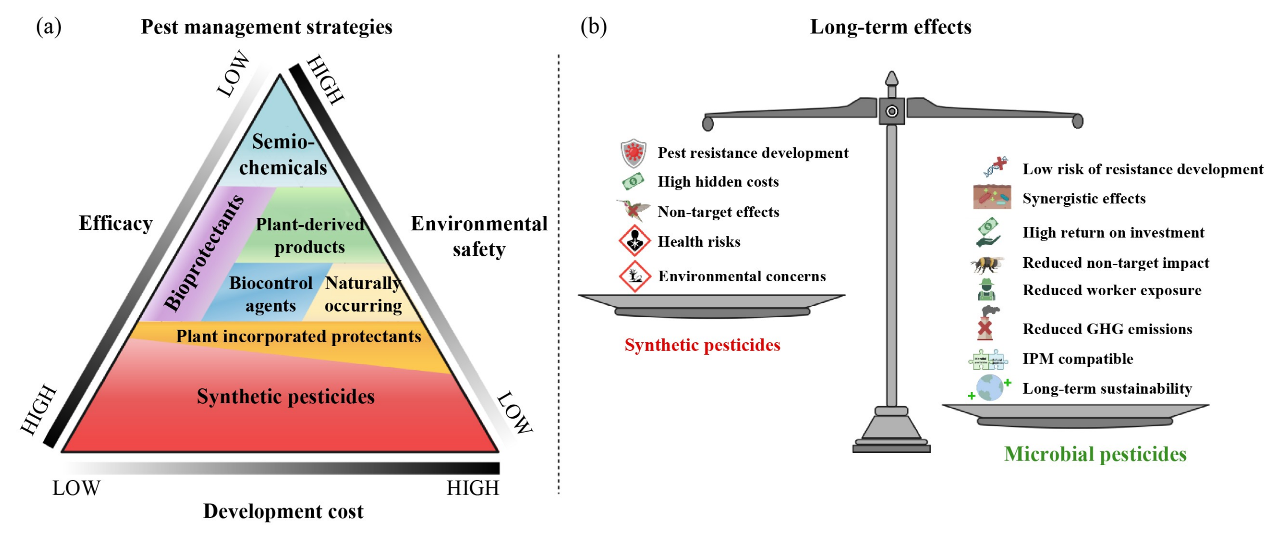


Fig. 5 A conceptual model comparing pest management strategies, including synthetic pesticides and biopesticides (biocontrol agents, bioprotectants, semiochemicals, plant-derived products, naturally occurring agents and plant-incorporated protectants). The figure illustrates (a) their relative short-term advantages in efficacy, development cost, and environmental safety, along with (b) their long-term monetary, agronomic and environmental impacts.

environmental stability and reduce application rates. Precision tools, such as nanosensors, can enable real-time monitoring of soil and plant health, thereby increasing decision-making accuracy and resource efficiency. These innovations, when aligned with ecological principles and adapted to local agricultural contexts can enhance the effectiveness and the field adoption of microbial solutions.

However, technical solutions alone are insufficient and must be accompanied by broader structural and institutional transformations. This includes the development of consistent international regulatory frameworks, expanded education and training and more equitable access to microbial technologies. Current regulatory models, which were developed primarily for chemical inputs often fail to accommodate the complex and context-dependent behavior of microbial agents. Also, the safe and effective application of emerging technologies, such as nanotechnology, will depend on regulatory standards that address biosafety, environmental compatibility and consumer trust.

Ultimately, microbial agents, such as endophytes, should not be viewed as mere biological inputs. They represent active contributors to the transformation of agriculture from input-intensive models to systems grounded in biological complexity and resilience. If their development is guided by extensive science, supportive policy, and integrated system design, they may surpass conventional inputs. In doing so, they can become a foundational component of sustainable agricultural intensification and a key contributor to global food security.

Acknowledgements

This research was supported by Genome Canada and Genome Québec (Genomics Applications Partnership Program, 6584), Canada Research Chairs Program (950-231770), Mathematics of Information Technology and Complex Systems Accelerate Program (IT29988) in partnership with Biosun Inc., Quality Assurance and Quality Control for Cannabis Program, McGill Graduate Excellence Award (90020), Centre de Recherche en Infectiologie Porcine et Avicole (RS-170946), and McGill Sustainability Systems Initiative Fellowship.

Compliance with ethics guidelines

Mohammad Jamil Kaddoura, Unnikrishnan Kannan, Laura Amaya Quiroz, and Saji George declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

REFERENCES

1. Savary S, Ficke A, Aubertot J N, Hollier C. Crop losses due to diseases and their implications for global food production losses and food security. *Food Security*, 2012, **4**(4): 519–537
2. Singh B K, Delgado-Baquerizo M, Egidi E, Guirado E, Leach J E, Liu H, Trivedi P. Climate change impacts on plant pathogens, food security and paths forward. *Nature Reviews. Microbiology*, 2023, **21**(10): 640–656
3. Khakimov A, Salakhutdinov I, Omolikov A, Utaganov S. Traditional and Current-prospective Methods of Agricultural Plant Diseases Detection: A Review. In: IOP Conference Series: Earth and Environmental Science. Bristol: *IOP publishing*, 2022, **951**(1): 012002
4. Davies C R, Wohlgemuth F, Young T, Violet J, Dickinson M, Sanders J W, Vallieres C, Avery S V. Evolving challenges and strategies for fungal control in the food supply chain. *Fungal Biology Reviews*, 2021, **36**: 15–26
5. Fisher M C, Hawkins N J, Sanglard D, Gurr S J. Worldwide emergence of resistance to antifungal drugs challenges human health and food security. *Science*, 2018, **360**(6390): 739–742
6. Avery S V, Singleton I, Magan N, Goldman G H. The fungal threat to global food security. *Fungal Biology*, 2019, **123**(8): 555–557
7. Moretti A, Logrieco A F, Susca A. Mycotoxins: an underhand food problem. In: Moretti A, Susca A, eds. Mycotoxigenic Fungi. New York, USA: *Springer*, 2016: 3–12
8. Eskola M, Kos G, Elliott C T, Hajšlová J, Mayar S, Krska R. Worldwide contamination of food-crops with mycotoxins: validity of the widely cited 'FAO estimate' of 25%. *Critical Reviews in Food Science and Nutrition*, 2020, **60**(16): 2773–2789
9. Park D L, Njapau H, Boutrif E. Minimizing risks posed by mycotoxins utilizing the HACCP concept. *Food, Nutrition*

and Agriculture, 1999(23): 49–54

10. Pitt J I, Miller J D. A concise history of mycotoxin research. *Journal of Agricultural and Food Chemistry*, 2017, **65**(33): 7021–7033
11. Hamad G M, Mehany T, Simal-Gandara J, Abou-Alella S, Esua O J, Abdel-Wahhab M A, Hafez E E. A review of recent innovative strategies for controlling mycotoxins in foods. *Food Control*, 2023, **144**: 109350
12. Khlangwiset P, Shephard G S, Wu F. Aflatoxins and growth impairment: a review. *Critical Reviews in Toxicology*, 2011, **41**(9): 740–755
13. Tola M, Kebede B. Occurrence, importance and control of mycotoxins: a review. *Cogent Food & Agriculture*, 2016, **2**(1): 1191103
14. Emadi A, Jayedi A, Mirmohammadkhani M, Abdolshahi A. Aflatoxin reduction in nuts by roasting, irradiation and fumigation: a systematic review and meta-analysis. *Critical Reviews in Food Science and Nutrition*, 2022, **62**(18): 5056–5066
15. Karlovsky P, Suman M, Berthiller F, De Meester J, Eisenbrand G, Perrin I, Oswald I P, Speijers G, Chiodini A, Recker T, Dussort P. Impact of food processing and detoxification treatments on mycotoxin contamination. *Mycotoxin Research*, 2016, **32**(4): 179–205
16. Fang L, Liao X, Jia B, Shi L, Kang L, Zhou L, Kong W. Recent progress in immunosensors for pesticides. *Biosensors & Bioelectronics*, 2020, **164**: 112255
17. Bernardes M F F, Pazin M, Pereira L C, Dorta D J. Impact of pesticides on environmental and human health. In: Andreazza A C, Scola G, eds. Toxicology Studies—Cells, Drugs and Environment. *InTech*, 2015
18. Yang M, Wang Y, Yang G, Wang Y, Liu F, Chen C. A review of cumulative risk assessment of multiple pesticide residues in food: current status, approaches and future perspectives. *Trends in Food Science & Technology*, 2024, **144**: 104340
19. Wang J Q, Hussain R, Ghaffar A, Afzal G, Saad A Q, Ahmad N, Nazir U, Ahmad H I, Hussain T, Khan A. Clinicohematological, mutagenic, and oxidative stress induced by pendimethalin in freshwater fish bighead carp (*Hypophthalmichthys nobilis*). *Oxidative Medicine and Cellular Longevity*, 2022, **2022**(1): 2093822
20. de Sousa Teixeira J R, de Souza A M, de Macedo-Sampaio J V, Menezes F P, Pereira B F, de Medeiros S R B, Luchiari A C. Embryotoxic effects of pesticides in zebrafish (*Danio rerio*): diflubenzuron, pyriproxyfen, and its mixtures. *Toxics*, 2024, **12**(2): 160
21. Rajak P, Ganguly A, Sarkar S, Mandi M, Dutta M, Podder S, Khatun S, Roy S. Immunotoxic role of organophosphates: an unseen risk escalating SARS-CoV-2 pathogenicity. *Food and Chemical Toxicology*, 2021, **149**: 112007
22. Piel C, Pouchieu C, Carles C, Béziat B, Boulanger M, Bureau M, Busson A, Grüber A, Lecluse Y, Migault L, Renier M, Rondeau V, Schwall X, Tual S, Pierre L, Baldi I, Arveux P, Bara S, Bouvier A M, Busquet T, Colonna M, Coureau G, Delanoé M, Grosclaude P, Guizard A V, Herbrecht P, Laplante J J, Lapotre-Ledoux B, Launoy G, Lenoir D, Marrer E, Marcotullio E, Maynadié M, Molinié F, Monnereau A, Paumier A, Pouzet P, Thibaudier J M, Troussard X, Velten M, Wavelet E, Woronoff A S. Agricultural exposures to carbamate herbicides and fungicides and central nervous system tumour incidence in the cohort AGRICAN. *Environment International*, 2019, **130**: 104876
23. Bourguet D, Guillemaud T. The hidden and external costs of pesticide use. In: Lichtfouse E, ed. Sustainable Agriculture Reviews. Cham: *Springer International Publishing*, 2016: 35–120
24. Borges S, Alkassab A T, Collison E, Hinarejos S, Jones B, McVey E, Roessink I, Steeger T, Sultan M, Wassenberg J. Overview of the testing and assessment of effects of microbial pesticides on bees: strengths, challenges and perspectives. *Apidologie*, 2021, **52**(6): 1256–1277
25. Marrone P G. Status of the biopesticide market and prospects for new bioherbicides. *Pest Management Science*, 2024, **80**(1): 81–86
26. Fusar Poli E, Fontefrancesco M F. Trends in the implementation of biopesticides in the Euro-Mediterranean region: a narrative literary review. *Sustainable Earth Reviews*, 2024, **7**(1): 14
27. Cai P, Dimopoulos G. Microbial biopesticides: a one health perspective on benefits and risks. *One Health*, 2025, **20**: 100962
28. Marrone P G. Status and potential of bioprotection products for crop protection. In: Maienfisch P, Stevenson TM, eds. Recent Highlights in the Discovery and Optimization of Crop Protection Products. Cambridge: *Elsevier*, 2021, 25–38.
29. Daraban G M, Hlihor R M, Suteu D. Pesticides *vs*. biopesticides: from pest management to toxicity and impacts on the environment and human health. *Toxics*, 2023, **11**(12): 983
30. Lebeda A, Luhová L, Sedlářová M, Jančová D. The role of enzymes in plant-fungal pathogens interactions / Die Rolle der Enzyme in den Beziehungen zwischen Pflanzen und pilzlichen Erregern. *Journal of Plant Diseases and Protection*, 2001, **108**(1): 89–111 (in German)
31. Annis S L, Goodwin P H. Recent advances in the molecular genetics of plant cell wall-degrading enzymes produced by plant pathogenic fungi. *European Journal of Plant Pathology*, 1997, **103**(1): 1–14
32. Knogge W. Fungal infection of plants. *Plant Cell*, 1996, **8**(10): 1711
33. Elmore J M, Coaker G. The role of the plasma membrane H^+-ATPase in plant–microbe interactions. *Molecular Plant*, 2011,

4(3): 416–427

34. Marra M, Camoni L, Visconti S, Fiorillo A, Evidente A. The surprising story of fusicoccin: a wilt-inducing phytotoxin, a tool in plant physiology and a 14-3-3-targeted drug. *Biomolecules*, 2021, **11**(9): 1393
35. Patel Z M, Mahapatra R, Jampala S S M. Role of fungal elicitors in plant defense mechanism. In: Sharma V, Salwan R, Al-Ani L K T, eds. Molecular Aspects of Plant Beneficial Microbes in Agriculture. Cambridge: *Academic Press*, 2020, 143–158
36. Hahn M, Mendgen K. Signal and nutrient exchange at biotrophic plant–fungus interfaces. *Current Opinion in Plant Biology*, 2001, **4**(4): 322–327
37. Wada M, Kato H, Malik K, Sriprasertsak P, Ichinose Y, Shiraishi T, Yamada T. A supprescin from a phytopathogenic fungus deactivates transcription of a plant defense gene encoding phenylalanine ammonia-lyase. *Journal of Molecular Biology*, 1995, **249**(3): 513–519
38. Thrall P H, Barrett L G, Dodds P N, Burdon J J. Epidemiological and evolutionary outcomes in gene-for-gene and matching allele models. *Frontiers in Plant Science*, 2015, **6**: 1084
39. Flor H H. Current status of the gene-for-gene concept. *Annual Review of Phytopathology*, 1971, **9**(1): 275–296
40. Kaur B, Bhatia D, Mavi G S. Eighty years of gene-for-gene relationship and its applications in identification and utilization of R genes. *Journal of Genetics*, 2021, **100**(2): 50
41. Laugé R, De Wit P J G M. Fungal avirulence genes: structure and possible functions. *Fungal Genetics and Biology*, 1998, **24**(3): 285–297
42. Rouxel T, Balesdent M H. Avirulence Genes. In: eLS. Chichester: *John Wiley & Sons Ltd*., 2010
43. Ferreira R B, Monteiro S, Freitas R, Santos C N, Chen Z, Batista L M, Duarte J, Borges A, Teixeira A R. Fungal pathogens: the battle for plant infection. *Critical Reviews in Plant Sciences*, 2006, **25**(6): 505–524
44. Kamle M, Borah R, Bora H, Jaiswal A K, Singh R K, Kumar P. Systemic acquired resistance (SAR) and induced systemic resistance (ISR): role and mechanism of action against phytopathogens. In: Hesham A L, Upadhyay R, Sharma G, Manoharachary C, Gupta V, eds. Fungal Biotechnology and Bioengineering. Cham: *Springer*, 2020, 457–470
45. Pieterse C M J, Zamioudis C, Berendsen R L, Weller D M, Van Wees S C M, Bakker P A H M. Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology*, 2014, **52**(1): 347–375
46. Boller T, Felix G. A renaissance of elicitors: perception of microbe-associated molecular patterns and danger signals by pattern-recognition receptors. *Annual Review of Plant Biology*, 2009, **60**(1): 379–406
47. Dodds P N, Rathjen J P. Plant immunity: towards an integrated view of plant–pathogen interactions. *Nature Reviews. Genetics*, 2010, **11**(8): 539–548
48. Prajapati S, Kumar N, Kumar S, Lakharan L, Maurya S. Biological control a sustainable approach for plant diseases management: a review. *Journal of Pharmacognosy and Phytochemistry*, 2020, **9**(2): 1514–1523
49. Choudhary D K, Prakash A, Johri B N. Induced systemic resistance (ISR) in plants: mechanism of action. *Indian Journal of Microbiology*, 2007, **47**(4): 289–297
50. Du Y, Han X, Tsuda K. Microbiome-mediated plant disease resistance: recent advances and future directions. *Journal of General Plant Pathology*, 2025, **91**(1): 1–17
51. Hassanisaadi M, Shahidi Bonjar G H, Hosseinipour A, Abdolshahi R, Ait Barka E, Saadoun I. Biological control of *Pythium aphanidermatum*, the causal agent of tomato root rot by two *Streptomyces* root symbionts. *Agronomy*, 2021, **11**(5): 846
52. Nazarov P A, Baleev D N, Ivanova M I, Sokolova L M, Karakozova M V. Infectious plant diseases: etiology, current status, problems and prospects in plant protection. *Acta Naturae*, 2020, **12**(3): 46–59
53. Afanasenko O S, Novozhilov K V. Problems of rational use of genetic resources of plants resistance to diseases. *Ekologicheskaia Genetika*, 2009, **7**(2): 38–43
54. Ramalingam J, Raveendra C, Savitha P, Vidya V, Chaithra T L, Velprabakaran S, Saraswathi R, Ramanathan A, Arumugam Pillai M P, Arumugachamy S, Vanniarajan C. Gene pyramiding for achieving enhanced resistance to bacterial blight, blast, and sheath blight diseases in rice. *Frontiers in Plant Science*, 2020, **11**: 591457
55. Haque M A, Rafii M Y, Yusoff M M, Ali N S, Yusuff O, Datta D R, Anisuzzaman M, Ikbal M F. Recent advances in rice varietal development for durable resistance to biotic and abiotic stresses through marker-assisted gene pyramiding. *Sustainability*, 2021, **13**(19): 10806
56. Zhou J, Peng Z, Long J, Sosso D, Liu B, Eom J S, Huang S, Liu S, Vera Cruz C, Frommer W B, White F F, Yang B. Gene targeting by the *TAL* effector PthXo2 reveals cryptic resistance gene for bacterial blight of rice. *Plant Journal*, 2015, **82**(4): 632–643
57. Malnoy M, Viola R, Jung M H, Koo O J, Kim S, Kim J S, Velasco R, Nagamangala Kanchiswamy C. DNA-free genetically edited grapevine and apple protoplast using CRISPR/Cas9 ribonucleoproteins. *Frontiers in Plant Science*, 2016, **7**: 1904
58. Ji X, Zhang H, Zhang Y, Wang Y, Gao C. Establishing a CRISPR–Cas-like immune system conferring DNA virus resistance in plants. *Nature Plants*, 2015, **1**(10): 15144
59. Fungicide Resistance Action Committee (FRAC). FRAC Code List 2025: Fungal Control Agents Sorted by Cross-resistance Pattern and Mode of Action (including Coding for FRAC

Groups on Product Labels). Brussels, Belgium: *FRAC*, 2025

60. Wade M, Delp C J. Aims and activities of industry's fungicide resistance action committee (FRAC). *EPPO Bulletin*, 1985, **15**(4): 577–583
61. Baibakova E V, Nefedjeva E E, Suska-Malawska M, Wilk M, Sevriukova G A, Zheltobriukhov V F. Modern fungicides: mechanisms of action, fungal resistance and phytotoxic effects. *Annual Research & Review in Biology*, 2019, **32**(3): 1–16
62. Stenzel K, Vors J P. Sterol biosynthesis inhibitors. In: Jeschke P, Witschel M, Kramer W, Schirmer U, eds. Modern Crop Protection Compounds. Weinheim: *Wiley-VCH*, 2019, 797–844
63. Kristoffersen R, Hansen A L, Munk L, Cedergreen N, Jørgensen L N. Management of beet rust in accordance with IPM principles. *Crop Protection)*, 2018, **111**: 6–16
64. Shang N, Yang Y, Xiao Y, Wu Y, Li K, Jiang X, Sanganyado E, Zhang Q, Xia X. Exposure levels and health implications of fungicides, neonicotinoid insecticides, triazine herbicides and their associated metabolites in pregnant women and men. *Environmental Pollution*, 2024, **342**: 123069
65. Ishii H. Impact of fungicide resistance in plant pathogens on crop disease control and agricultural environment. *Japan Agricultural Research Quarterly*, 2006, **40**(3): 205–211
66. Hoffmeister M, Scheu P, Glaab A, Zito R, Stammler G. Sensitivity evolution in *Venturia inaequalis* towards SDHIs in comparison to other modes of action. *European Journal of Plant Pathology*, 2024, **168**(4): 763–773
67. Juroszek P, von Tiedemann A. Potential strategies and future requirements for plant disease management under a changing climate. *Plant Pathology*, 2011, **60**(1): 100–112
68. Bueno A F, Sutil W P, Jahnke S M, Carvalho G A, Cingolani M F, Colmenarez Y C, Corniani N. Biological control as part of the soybean integrated pest management (IPM): potential and challenges. *Agronomy*, 2023, **13**(10): 2532
69. Jørgensen L N, Matzen N, Leitzke R, Thomas J E, O'Driscoll A, Klocke B, Maumene C, Lindell I, Wahlquist K, Zemeca L, Apesteguia M B, Randazzo B, Slikova S, Holdgate S. Management of rust in wheat using IPM principles and alternative products. *Agriculture*, 2024, **14**(6): 821
70. Collinge D B, Jensen D F, Rabiey M, Sarrocco S, Shaw M W, Shaw R H. Biological control of plant diseases—What has been achieved and what is the direction? *Plant Pathology*, 2022, **71**(5): 1024–1047
71. Baker K F, Cook R J. Biological Control of Plant Pathogens. San Francisco: *WH Freeman and Company*, 1974
72. De Silva N I, Brooks S, Lumyong S, Hyde K D. Use of endophytes as biocontrol agents. *Fungal Biology Reviews*, 2019, **33**(2): 133–148
73. Abdollahdokht D, Gao Y, Faramarz S, Poustforoosh A, Abbasi M, Asadikaram G, Nematollahi M H. Conventional agrochemicals towards nano-biopesticides: an overview on recent advances. *Chemical and Biological Technologies in Agriculture*, 2022, **9**(1): 13
74. Saritha M, Prasad Tollamadugu N V K V. The status of research and application of biofertilizers and biopesticides: global scenario. In: Buddolla V, ed. Recent Developments in Applied Microbiology and Biochemistry. *Academic Press*, 2019, 195–207
75. Jhala J, Baloda A S, Rajput V S. Role of bio-pesticides in recent trends of insect pest management: a review. *Journal of Pharmacognosy and Phytochemistry*, 2020, **9**(1): 2237–2240
76. Stenberg J A, Sundh I, Becher P G, Björkman C, Dubey M, Egan P A, Friberg H, Gil J F, Jensen D F, Jonsson M, Karlsson M, Khalil S, Ninkovic V, Rehermann G, Vetukuri R R, Viketoft M. When is it biological control? A framework of definitions, mechanisms, and classifications. *Journal of Pest Science*, 2021, **94**(3): 665–676
77. Kiss L, Russell J C, Szentiványi O, Xu X, Jeffries P. Biology and biocontrol potential of *Ampelomyces* mycoparasites, natural antagonists of powdery mildew fungi. *Biocontrol Science and Technology*, 2004, **14**(7): 635–651
78. Santoyo G, del Carmen Orozco-Mosqueda M, Govindappa M. Mechanisms of biocontrol and plant growth-promoting activity in soil bacterial species of *Bacillus* and *Pseudomonas*: a review. *Biocontrol Science and Technology*, 2012, **22**(8): 855–872
79. Kerr A. Biological control of crown gall through production of agrocin 84. *Plant Disease*, 1980, **64**(1): 24–25, 28–30
80. Reetha A K, Pavani S L, Mohan S. Hydrogen cyanide production ability by bacterial antagonist and their antibiotics inhibition potential on *Macrophomina phaseolina* (Tassi.) Goid. *International Journal of Current Microbiology and Applied Sciences*, 2014, **3**(5): 172–178
81. Moyne A L, Shelby R, Cleveland T E, Tuzun S. Bacillomycin D: an iturin with antifungal activity against *Aspergillus flavus*. *Journal of Applied Microbiology*, 2001, **90**(4): 622–629
82. Kloepper J W, Leong J, Teintze M, Schroth M N. *Pseudomonas* siderophores: a mechanism explaining disease-suppressive soils. *Current Microbiology*, 1980, **4**(5): 317–320
83. Leclère V, Béchet M, Adam A, Guez J S, Wathelet B, Ongena M, Thonart P, Gancel F, Chollet-Imbert M, Jacques P. Mycosubtilin overproduction by *Bacillus subtilis* BBG100 enhances the organism's antagonistic and biocontrol activities. *Applied and Environmental Microbiology*, 2005, **71**(8): 4577–4584
84. Boland G J. Fungal viruses, hypovirulence, and biological control of *Sclerotinia* species. *Canadian Journal of Plant Pathology*, 2004, **26**(1): 6–18
85. Olivé M, Campo S. The dsRNA mycovirus ChNRV1 causes mild hypervirulence in the fungal phytopathogen *Colletotrichum higginsianum*. *Archives of Microbiology*, 2021,

203(1): 241–249

86. Aihara M, Urayama S I, Le M T, Katoh Y, Higashiura T, Fukuhara T, Arie T, Teraoka T, Komatsu K, Moriyama H. Infection by *Magnaporthe oryzae* chrysovirus 1 strain A triggers reduced virulence and pathogenic race conversion of its host fungus. *Magnaporthe oryzae*. *Journal of General Plant Pathology*, 2018, **84**(2): 92–103
87. Vero S, Garmendia G, Allori E, Sanz J M, Gonda M, Alconada T, Cavello I, Dib J R, Diaz M A, Nally C, Pimenta R S, da Silva J F M, Vargas M, Zaccari F, Wisniewski M. Microbial biopesticides: diversity, scope, and mechanisms involved in plant disease control. *Diversity*, 2023, **15**(3): 457
88. Nawrocka J, Małolepsza U. Diversity in plant systemic resistance induced by *Trichoderma*. *Biological Control*, 2013, **67**(2): 149–156
89. Bakker P A H M, Ran L X, Pieterse C M J, van Loon L C. Understanding the involvement of rhizobacteria-mediated induction of systemic resistance in biocontrol of plant diseases. *Canadian Journal of Plant Pathology*, 2003, **25**(1): 5–9
90. Kloepper J W, Ryu C M, Zhang S. Induced systemic resistance and promotion of plant growth by *Bacillus* spp. *Phytopathology*, 2004, **94**(11): 1259–1266
91. van Loon L C, Bakker P A, Pieterse C M. Systemic resistance induced by rhizosphere bacteria. *Annual Review of Phytopathology*, 1998, **36**(1): 453–483
92. Ni H, Kong W L, Zhang Q Q, Wu X Q. Volatiles emitted by *Pseudomonas aurantiaca* ST-TJ4 trigger systemic plant resistance to *Verticillium dahliae*. *Microbiological Research*, 2024, **287**: 127834
93. Larran S, Simón M R, Moreno M V, Santamarina Siurana M P, Perelló A. Endophytes from wheat as biocontrol agents against Tan spot disease. *Biological Control*, 2016, **92**: 17–23
94. Suárez-Estrella F, Arcos-Nievas M A, López M J, Vargas-García M C, Moreno J. Biological control of plant pathogens by microorganisms isolated from agro-industrial composts. *Biological Control*, 2013, **67**(3): 509–515
95. Vinale F, Sivasithamparam K, Ghisalberti E L, Marra R, Woo S L, Lorito M. *Trichoderma*–plant–pathogen interactions. *Soil Biology & Biochemistry*, 2008, **40**(1): 1–10
96. Card S D, Walter M, Jaspers M V, Sztejnberg A, Stewart A. Targeted selection of antagonistic microorganisms for control of *Botrytis cinerea* of strawberry in New Zealand. *Australasian Plant Pathology*, 2009, **38**(2): 183–192
97. Huang N, Jin X, Wen J T, Zhang Y F, Yang X, Wei G Y, Wang Y K, Qin M. Biocontrol and growth promotion potential of *Bacillus subtilis* CTXW 7–6-2 against *Rhizoctonia solani* that causes tobacco target spot disease. *Polish Journal of Microbiology*, 2024, **73**(1): 29–38
98. Yang F, Wang X, Jiang H, Yao Q, Liang S, Chen W, Shi G, Tian B, Hegazy A, Ding S. Mechanism of a novel *Bacillus subtilis* JNF2 in suppressing *Fusarium oxysporum* f. sp. *cucumerium* and enhancing cucumber growth. *Frontiers in Microbiology*, 2024, **15**: 1459906
99. Takeuchi K, Ogiso M, Ota A, Nishimura K, Nishino C, Omori Y, Maeda M, Mizui R, Yamanaka H, Ogino T, Seo S. *Pseudomonas rhodesiae* HAI-0804 suppresses *Pythium* damping off and root rot in cucumber by its efficient root colonization promoted by amendment with glutamate. *Frontiers in Microbiology*, 2024, **15**: 1485167
100. Ma W, Tang S, Dengzeng Z, Zhang D, Zhang T, Ma X. Root exudates contribute to belowground ecosystem hotspots: a review. *Frontiers in Microbiology*, 2022, **13**: 937940
101. Trivedi P, Leach J E, Tringe S G, Sa T, Singh B K. Plant–microbiome interactions: from community assembly to plant health. *Nature Reviews. Microbiology*, 2020, **18**(11): 607–621
102. Vandenkoornhuyse P, Quaiser A, Duhamel M, Van A L, Dufresne A. The importance of the microbiome of the plant holobiont. *New Phytologist*, 2015, **206**(4): 1196–1206
103. Astudillo-García C, Bell J J, Webster N S, Glasl B, Jompa J, Montoya J M, Taylor M W. Evaluating the core microbiota in complex communities: a systematic investigation. *Environmental Microbiology*, 2017, **19**(4): 1450–1462
104. Lemanceau P, Blouin M, Muller D, Moënne-Loccoz Y. Let the core microbiota be functional. *Trends in Plant Science*, 2017, **22**(7): 583–595
105. Omomowo O I, Babalola O O. Bacterial and fungal endophytes: tiny giants with immense beneficial potential for plant growth and sustainable agricultural productivity. *Microorganisms*, 2019, **7**(11): 481
106. Schulz B J E, Boyle C J C, Sieber T N. Microbial Root Endophytes. Berlin, Heidelberg: *Springer*, 2006
107. De Souza J T, Silva A C M, de Jesus Santos A F, Santos P O, Alves P S, Cruz-Magalhães V, Santos Marbach P A, Loguercio L L. Endophytic bacteria isolated from both healthy and diseased *Agave sisalana* plants are able to control the Bole rot disease. *Biological Control*, 2021, **157**: 104575
108. Dwibedi V, Rath S K, Joshi M, Kaur R, Kaur G, Singh D, Kaur G, Kaur S. Microbial endophytes: application towards sustainable agriculture and food security. *Applied Microbiology and Biotechnology*, 2022, **106**(17): 5359–5384
109. Tewari S, Shrivas V L, Hariprasad P, Sharma S. Harnessing endophytes as biocontrol agents. In: Ali Ansari R, Mahmood I, eds. Plant Health Under Biotic Stress. Singapore: *Springer*, 2019, 189–218
110. Wani Z A, Ashraf N, Mohiuddin T, Riyaz-Ul-Hassan S. Plant-endophyte symbiosis, an ecological perspective. *Applied Microbiology and Biotechnology*, 2015, **99**(7): 2955–2965
111. Phurailatpam L, Gupta A, Sahu P K, Mishra S. Inoculation with native bacterial endophytes promote adventitious rooting and plant growth in *Piper longum* L. *Symbiosis*, 2024,

93(2): 229–240

112. Amaradasa B S, Mei C, He Y, Chretien R L, Doss M, Durham T, Lowman S. Biocontrol potential of endophytic *Pseudomonas* strain IALR1619 against two *Pythium* species in cucumber and hydroponic lettuce. *PLoS One*, 2024, **19**(2): e0298514
113. Zulfiqar F, Moosa A, Ali H M, Bermejo N F, Munné-Bosch S. Biostimulants: a sufficiently effective tool for sustainable agriculture in the era of climate change. *Plant Physiology and Biochemistry*, 2024, **211**: 108699
114. Ruzzi M, Colla G, Rouphael Y. Editorial: biostimulants in agriculture II: towards a sustainable future. *Frontiers in Plant Science*, 2024, **15**: 1427283
115. Olanrewaju O S, Glick B R, Babalola O O. Mechanisms of action of plant growth promoting bacteria. *World Journal of Microbiology & Biotechnology*, 2017, **33**(11): 197
116. Baas P, Mohan J E, Markewitz D, Knoepp J D. Assessing heterogeneity in soil nitrogen cycling: a plot-scale approach. *Soil Science Society of America Journal*, 2014, **78**(S1): S237–S247
117. Cocking E C. Endophytic colonization of plant roots by nitrogen-fixing bacteria. *Plant and Soil*, 2003, **252**(1): 169–175
118. Masson-Boivin C, Sachs J L. Symbiotic nitrogen fixation by rhizobia—The roots of a success story. *Current Opinion in Plant Biology*, 2018, **44**: 7–15
119. Santoyo G, Moreno-Hagelsieb G, del Carmen Orozco-Mosqueda M, Glick B R. Plant growth-promoting bacterial endophytes. *Microbiological Research*, 2016, **183**: 92–99
120. Vandana U K, Rajkumari J, Singha L P, Satish L, Alavilli H, Sudheer P D V N, Chauhan S, Ratnala R, Satturu V, Mazumder P B, Pandey P. The endophytic microbiome as a hotspot of synergistic interactions, with prospects of plant growth promotion. *Biology*, 2021, **10**(2): 101
121. Alori E T, Glick B R, Babalola O O. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Frontiers in Microbiology*, 2017, **8**: 971
122. Oteino N, Lally R D, Kiwanuka S, Lloyd A, Ryan D, Germaine K J, Dowling D N. Plant growth promotion induced by phosphate solubilizing endophytic *Pseudomonas isolates*. *Frontiers in Microbiology*, 2015, **6**: 745
123. Rodríguez H, Fraga R. Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances*, 1999, **17**(4–5): 319–339
124. Khan A A, Jilani G, Akhter M S, Naqvi S M, Rasheed M. Phosphorus solubilizing bacteria: occurrence, mechanisms and their role in crop production. *Journal of Agricultural and Biological Science*, 2019, **1**: 48–58
125. Banerjee M R, Yesmin L, Vessey J K, Rai M. Plant-growth-promoting rhizobacteria as biofertilizers and biopesticides. In: Rai M, ed. Handbook of Microbial Biofertilizers. New York: *Food Products Press*, 2006, 137–181
126. Saharan B S, Nehra V. Plant growth promoting rhizobacteria (PGPR): a critical review. *Life Science Medical Research*, 2011, **21**: 1–30
127. Spaepen S, Versées W, Gocke D, Pohl M, Steyaert J, Vanderleyden J. Characterization of phenylpyruvate decarboxylase, involved in auxin production of *Azospirillum brasilense*. *Journal of Bacteriology*, 2007, **189**(21): 7626–7633
128. Remans R, Beebe S, Blair M, Manrique G, Tovar E, Rao I, Croonenborghs A, Torres-Gutierrez R, El-Howeity M, Michiels J, Vanderleyden J. Physiological and genetic analysis of root responsiveness to auxin-producing plant growth-promoting bacteria in common bean (*Phaseolus vulgaris* L.). *Plant and Soil*, 2008, **302**: 149–161
129. Ali B, Hasnain S. Potential of bacterial indoleacetic acid to induce adventitious shoots in plant tissue culture. *Letters in Applied Microbiology*, 2007, **45**(2): 128–133
130. Spaepen S, Vanderleyden J, Remans R. Indole-3-acetic acid in microbial and microorganism-plant signaling. *FEMS Microbiology Reviews*, 2007, **31**(4): 425–448
131. Glick B R. Plant growth-promoting bacteria: mechanisms and applications. *Scientifica*, 2012, **2012**: 963401
132. Defez R, Andreozzi A, Bianco C. The overproduction of indole-3-acetic acid (IAA) in endophytes upregulates nitrogen fixation in both bacterial cultures and inoculated rice plants. *Microbial Ecology*, 2017, **74**(2): 441–452
133. Ji S H, Gururani M A, Chun S C. Isolation and characterization of plant growth promoting endophytic diazotrophic bacteria from Korean rice cultivars. *Microbiological Research*, 2014, **169**(1): 83–98
134. Abeles F B, Morgan P W, Saltveit M E Jr. Ethylene in Plant Biology. 2nd ed. San Diego: *Academic Press*, 2012
135. Glick B R, Cheng Z, Czarny J, Duan J. Promotion of plant growth by ACC deaminase-producing soil bacteria. In: Bakker P A H M, Raaijmakers J M, Bloemberg G, Höfte M, Lemanceau P, Cooke B M, eds. New Perspectives and Approaches in Plant Growth-Promoting Rhizobacteria Research. Dordrecht, Netherlands: *Springer*, 2007, 329–339
136. Saha R, Saha N, Donofrio R S, Bestervelt L L. Microbial siderophores: a mini review. *Journal of Basic Microbiology*, 2013, **53**(4): 303–317
137. Walitang D I, Kim K, Madhaiyan M, Kim Y K, Kang Y, Sa T. Characterizing endophytic competence and plant growth promotion of bacterial endophytes inhabiting the seed endosphere of Rice. *BMC Microbiology*, 2017, **17**(1): 209
138. Wilson M K, Abergel R J, Arceneaux J E L, Raymond K N, Byers B R. Temporal production of the two *Bacillus anthracis* siderophores, petrobactin and bacillibactin. *Biometals*, 2010, **23**(1): 129–134
139. Ramette A, Moënne-Loccoz Y, Défago G. Genetic diversity and biocontrol potential of fluorescent pseudomonads producing phloroglucinols and hydrogen cyanide from Swiss

soils naturally suppressive or conducive to *Thielaviopsis basicola* -mediated-mediated black root rot of tobacco. *FEMS Microbiology Ecology*, 2006, **55**(3): 369–381

140. Das K, Prasanna R, Saxena A K. Rhizobia: a potential biocontrol agent for soilborne fungal pathogens. *Folia Microbiologica*, 2017, **62**(5): 425–435
141. Zachow C, Müller H, Monk J, Berg G. Complete genome sequence of *Pseudomonas brassicacearum* strain L13-6-12, a biological control agent from the rhizosphere of potato. *Standards in Genomic Sciences*, 2017, **12**(1): 6
142. Goswami D, Thakker J N, Dhandhukia P C. Portraying mechanics of plant growth promoting rhizobacteria (PGPR): a review. *Cogent Food & Agriculture*, 2016, **2**(1): 1127500
143. Guo B, Wang Y, Sun X, Tang K. Bioactive natural products from endophytes: a review. *Applied Biochemistry and Microbiology*, 2008, **44**(2): 136–142
144. Zia M A, Riaz R, Batool A, Yasmin H, Nosheen A, Naz R, Hassan M N. Glucanolytic rhizobacteria associated with wheat- maize cropping system suppress the *Fusarium* wilt of tomato (*Lycopersicum esculentum* L). *Scientia Horticulturae*, 2021, **287**: 110275
145. Saberi Riseh R, Vatankhah M, Hassanisaadi M, Barka E A. Unveiling the role of hydrolytic enzymes from soil biocontrol bacteria in sustainable phytopathogen management. *Frontiers in Bioscience (Landmark Edition)*, 2024, **29**(3): 105
146. Reddy E C, Reddy G S, Goudar V, Sriramula A, Swarnalatha G V, Al Tawaha A R M, Sayyed R Z. Hydrolytic enzyme producing plant growth-promoting rhizobacteria (PGPR) in plant growth promotion and biocontrol. In: Sayyed R Z, Uarrota V G, eds. Secondary Metabolites and Volatiles of PGPR in Plant-Growth Promotion. Cham: *Springer International Publishing*, 2022, 303–312
147. Tripathi S, Kamal S, Sheramati I, Oelmuller R, Varma A. Mycorrhizal fungi and other root endophytes as biocontrol agents against root pathogens. In: Varma A, ed. *Mycorrhiza*. Berlin, Heidelberg: *Springe*r, 2008: 281–306
148. Khare E, Yadav A. The role of microbial enzyme systems in plant growth promotion. *Climate Change and Environmental Sustainability*, 2017, **5**(2): 122
149. Jadhav H, Sayyed R. Hydrolytic enzymes of rhizospheric microbes in crop protection. *MOJ Cell Science & Report*, 2016, **3**(5): 135–136
150. Farag M A, Zhang H, Ryu C M. Dynamic chemical communication between plants and bacteria through airborne signals: induced resistance by bacterial volatiles. *Journal of Chemical Ecology*, 2013, **39**(7): 1007–1018
151. del Rosario Cappellari L, Chiappero J, Banchio E. Invisible signals from the underground: a practical method to investigate the effect of microbial volatile organic compounds emitted by rhizobacteria on plant growth. *Biochemistry and Molecular Biology Education*, 2019, **47**(4): 388–393
152. Xie S, Liu J, Gu S, Chen X, Jiang H, Ding T. Antifungal activity of volatile compounds produced by endophytic *Bacillus subtilis* DZSY21 against *Curvularia lunata*. *Annals of Microbiology*, 2020, **70**(1): 2
153. Gao Z, Zhang B, Liu H, Han J, Zhang Y. Identification of endophytic *Bacillus velezensis* ZSY-1 strain and antifungal activity of its volatile compounds against *Alternaria solani* and *Botrytis cinerea*. *Biological Control*, 2017, **105**: 27–39
154. Gutiérrez-Luna F M, López-Bucio J, Altamirano-Hernández J, Valencia-Cantero E, de la Cruz H R, Macías-Rodríguez L. Plant growth-promoting rhizobacteria modulate root-system architecture in *Arabidopsis thaliana* through volatile organic compound emission. *Symbiosis*, 2010, **51**(1): 75–83
155. Rutherford S T, Bassler B L. Bacterial quorum sensing: its role in virulence and possibilities for its control. *Cold Spring Harbor Perspectives in Medicine*, 2012, **2**(11): a012427
156. Novick R P, Geisinger E. Quorum sensing in *Staphylococci*. *Annual Review of Genetics*, 2008, **42**(1): 541–564
157. Miller M B, Bassler B L. Quorum sensing in bacteria. *Annual Review of Microbiology*, 2001, **55**(1): 165–199
158. Wei Y, Perez L J, Ng W L, Semmelhack M F, Bassler B L. Mechanism of *Vibrio cholerae* autoinducer-1 biosynthesis. *ACS Chemical Biology*, 2011, **6**(4): 356–365
159. Blair P M, Land M L, Piatek M J, Jacobson D A, Lu T S, Doktycz M J, Pelletier D A. Exploration of the biosynthetic potential of the *Populus* microbiome. *mSystems*, 2018, **3**(5): e00045–18
160. Ahmed A, Liu Y, He P, He P, Wu Y, Munir S, He Y. *Bacillus* quorum quenching shapes the *Citrus* mycobiome through interKingdom signaling. *Science of the Total Environment*, 2024, **956**: 177074
161. Paul E, Sharma C, Chaturvedi P, Bhatnagar P. Quorum quenching activity of endophytic *Bacillus* sp. EBS9 from *Tecomella undulata* and its biocontrol applications. *Current Research in Microbial Sciences*, 2024, **7**: 100307
162. Chagas F O, de Cassia Pessotti R, Caraballo-Rodríguez A M, Pupo M T. Chemical signaling involved in plant–microbe interactions. *Chemical Society Reviews*, 2018, **47**(5): 1652–1704
163. Gurjar M S, Ali S, Akhtar M, Singh K S. Efficacy of plant extracts in plant disease management. *Agricultural Sciences*, 2012, **3**(3): 425–433
164. Kumar K K, Sridhar J, Murali-Baskaran R K, Senthil-Nathan S, Kaushal P, Dara S K, Arthurs S. Microbial biopesticides for insect pest management in India: current status and future prospects. *Journal of Invertebrate Pathology*, 2019, **165**: 74–81
165. Batista B D, Singh B K. Realities and hopes in the application of microbial tools in agriculture. *Microbial Biotechnology*, 2021, **14**(4): 1258–1268
166. Essiedu J A, Adepoju F O, Ivantsova M N. Benefits and limitations in using biopesticides: a review. *The Vii*

International Young Researchers' Conference-Physics, Technology, Innovations (*Pti-2020*), 2020, **2313**: 080002

167. Bonaterra A, Badosa E, Daranas N, Francés J, Roselló G, Montesinos E. Bacteria as biological control agents of plant diseases. *Microorganisms*, 2022, **10**(9): 1759
168. Kumar V, Ahluwalia V, Saran S, Kumar J, Patel A K, Singhania R R. Recent developments on solid-state fermentation for production of microbial secondary metabolites: challenges and solutions. *Bioresource Technology*, 2021, **323**: 124566
169. Le Cocq K, Gurr S J, Hirsch P R, Mauchline T H. Exploitation of endophytes for sustainable agricultural intensification. *Molecular Plant Pathology*, 2017, **18**(3): 469–473
170. Robinson R J, Fraaije B A, Clark I M, Jackson R W, Hirsch P R, Mauchline T H. Wheat seed embryo excision enables the creation of axenic seedlings and Koch's postulates testing of putative bacterial endophytes. *Scientific Reports*, 2016, **6**(1): 25581
171. O'Callaghan M. Microbial inoculation of seed for improved crop performance: issues and opportunities. *Applied Microbiology and Biotechnology*, 2016, **100**(13): 5729–5746
172. Chhipa H. Mycosynthesis of nanoparticles for smart agricultural practice: a green and eco-friendly approach. In: Shukla A K, Iravani S, eds. Green Synthesis, Characterization and Applications of Nanoparticles. Amsterdam: *Elsevier*, 2019, 87–109
173. Khan M R, Rizvi T F. Nanotechnology: scope and application in plant disease management. *Plant Pathology Journal*, 2014, **13**(3): 214–231
174. Singh K R, Nayak V, Sarkar T, Singh R P. Cerium oxide nanoparticles: properties, biosynthesis and biomedical application. *RSC Advances*, 2020, **10**(45): 27194–27214
175. Abarca-Cabrera L, Fraga-García P, Berensmeier S. Bio-nano interactions: binding proteins, polysaccharides, lipids and nucleic acids onto magnetic nanoparticles. *Biomaterials Research*, 2021, **25**(1): 12
176. Zulfiqar F, Navarro M, Ashraf M, Akram N A, Munné-Bosch S. Nanofertilizer use for sustainable agriculture: advantages and limitations. *Plant Science*, 2019, **289**: 110270
177. Chhipa H. Nanofertilizers and nanopesticides for agriculture. *Environmental Chemistry Letters*, 2017, **15**(1): 15–22
178. Weisany W, Razmi J, Pashang D. Improving seed germination and physiological characteristics of maize seedlings under osmotic stress through potassium nano-silicate treatment. *Frontiers in Plant Science*, 2023, **14**: 1274396
179. Esper Neto M, Britt D W, Lara L M, Cartwright A, dos Santos R F, Inoue T T, Batista M A. Initial development of corn seedlings after seed priming with nanoscale synthetic zinc oxide. *Agronomy*, 2020, **10**(2): 307
180. Nongbet A, Mishra A K, Mohanta Y K, Mahanta S, Ray M K, Khan M, Baek K H, Chakrabartty I. Nanofertilizers: a smart and sustainable attribute to modern agriculture. *Plants*, 2022, **11**(19): 2587
181. Kalwani M, Chakdar H, Srivastava A, Pabbi S, Shukla P. Effects of nanofertilizers on soil and plant-associated microbial communities: emerging trends and perspectives. *Chemosphere*, 2022, **287**: 132107
182. Worrall E, Hamid A, Mody K, Mitter N, Pappu H. Nanotechnology for plant disease management. *Agronomy*, 2018, **8**(12): 285
183. Mustafa I F, Hussein M Z. Synthesis and technology of nanoemulsion-based pesticide formulation. *Nanomaterials*, 2020, **10**(8): 1608
184. Benelli G. Mode of action of nanoparticles against insects. *Environmental Science and Pollution Research International*, 2018, **25**(13): 12329–12341
185. Kim S W, Jung J H, Lamsal K, Kim Y S, Min J S, Lee Y S. Antifungal effects of silver nanoparticles (AgNPs) against various plant pathogenic fungi. *Mycobiology*, 2012, **40**(1): 53–58
186. Singh B K, Tiwari S, Dubey N K. Essential oils and their nanoformulations as green preservatives to boost food safety against mycotoxin contamination of food commodities: a review. *Journal of the Science of Food and Agriculture*, 2021, **101**(12): 4879–4890
187. Feng J, Chen W, Liu Q, Chen Z, Yang J, Yang W. Development of abamectin-loaded nanoemulsion and its insecticidal activity and cytotoxicity. *Pest Management Science*, 2020, **76**(12): 4192–4201
188. Saifullah M, Shishir M R I, Ferdowsi R, Tanver Rahman M R, Van Vuong Q. Micro and nano encapsulation, retention and controlled release of flavor and aroma compounds: a critical review. *Trends in Food Science & Technology*, 2019, **86**: 230–251
189. Shishir M R I, Xie L, Sun C, Zheng X, Chen W. Advances in micro and nano-encapsulation of bioactive compounds using biopolymer and lipid-based transporters. *Trends in Food Science & Technology*, 2018, **78**: 34–60
190. Jeyakumari A, Zynudheen A A, Parvathy U. Microencapsulation of bioactive food ingredients and controlled release—A review. *MOJ Food Processing & Technology*, 2016, **2**(6): 214–224
191. Zabot G L, Schaefer Rodrigues F, Polano Ody L, Vinícius Tres M, Herrera E, Palacin H, Córdova-Ramos J S, Best I, Olivera-Montenegro L. Encapsulation of bioactive compounds for food and agricultural applications. *Polymers*, 2022, **14**(19): 4194
192. Panichikkal J, Prathap G, Nair R A, Krishnankutty R E. Evaluation of plant probiotic performance of *Pseudomonas* sp. encapsulated in alginate supplemented with salicylic acid and zinc oxide nanoparticles. *International Journal of Biological Macromolecules*, 2021, **166**: 138–143

193. Young C C, Rekha P D, Lai W A, Arun A B. Encapsulation of plant growth-promoting bacteria in alginate beads enriched with humic acid. *Biotechnology and Bioengineering*, 2006, **95**(1): 76–83

194. Taban A, Saharkhiz M J, Kavoosi G. Development of pre-emergence herbicide based on Arabic gum-gelatin, apple pectin and savory essential oil nano-particles: a potential green alternative to metribuzin. *International Journal of Biological Macromolecules*, 2021, **167**: 756–765

195. Krastev V, Stoyanova N, Valcheva I, Draganova D, Spasova M, Stoilova O. Encapsulation of *Bacillus subtilis* in chitosan gel beads for eco-friendly crop protection. *Gels*, 2025, **11**(4): 302

196. Lodi L A, Borges R, Lopes M M, Graciano V A, Bortoletto-Santos R, Barud H S, de Oliveira-Paiva C A, Ribeiro C, Farinas C S. Spray-drying microencapsulation of *Bacillus megaterium* in PVA/cationic starch/zinc oxide for promoting growth and zinc availability in soybean plants. *ACS Agricultural Science & Technology*, 2024, **4**(12): 1271–1283

197. Moradi Pour M, Hassanisaadi M, Kennedy J F, Saberi Riseh R. A novel biopolymer technique for encapsulation of *Bacillus velezensis* BV9 into double coating biopolymer made by in alginate and natural gums to biocontrol of wheat take-all disease. *International Journal of Biological Macromolecules*, 2024, **257**: 128526

198. Chevalier Y, Bolzinger M A. Emulsions stabilized with solid nanoparticles: Pickering emulsions. *Colloids and Surfaces. A, Physicochemical and Engineering Aspects*, 2013, **439**: 23–34

199. Harman C L G, Patel M A, Guldin S, Davies G L. Recent developments in Pickering emulsions for biomedical applications. *Current Opinion in Colloid & Interface Science*, 2019, **39**: 173–189

200. de Oca-Ávalos J M M, Candal R J, Herrera M L. Nanoemulsions: stability and physical properties. *Current Opinion in Food Science*, 2017, **16**: 1–6

201. Xie H, Zhao W, Zhang X, Wang Z. Demulsification of bacteria-stabilized Pickering emulsions using modified silica nanoparticles. *ACS Applied Materials & Interfaces*, 2022, **14**(21): 24102–24112

202. Yaakov N, Kottakota C, Mani K A, Naftali S M, Zelinger E, Davidovitz M, Ment D, Mechrez G. Encapsulation of *Bacillus thuringiensis* in an inverse Pickering emulsion for pest control applications. *Colloids and Surfaces. B, Biointerfaces*, 2022, **213**: 112427

203. Kishorkumar C, Harish S, Karthikeyan G, Sharmila D J S, Nivedha M. Harnessing nanoencapsulated *Bacillus* spp. consortia to combat groundnut bud necrosis *Orthotospovirus* in tomato. *ACS Applied Materials & Interfaces*, 2024, **16**(9): 11185–11193

204. Campaña J M, Arias M. Nanofibers as a delivery system for arbuscular mycorrhizal fungi. *ACS Applied Polymer Materials*, 2020, **2**(11): 5033–5038

205. Stoyanova N, Nachev N, Naydenov M, Valcheva I, Spasova M, Stoilova O. Biocontrol potential of poly(3-hydroxybutyrate) fibers functionalized with chitooligosaccharide/*Bacillus subtilis* using electrospinning and electrospraying. *Polymers*, 2025, **17**(5): 692