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# Exploring the Role of Lactic Acid Bacteria (LAB) in Plant Disease Management and Crop Growth Enhancement: A Concise Review

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## Abstract

In the realm of agriculture, microbial diseases pose a substantial threat, leading to substantial losses in crop yield and quality. Traditional approaches to combat these microbiological threats have often relied on chemical control agents such as pesticides, herbicides, and insecticides. However, the overuse of these chemicals has given rise to unintended consequences, including agricultural quality deterioration, environmental degradation, and risks to human health. These chemical agents persist in the soil and environment long after their intended application, resisting natural decomposition. In response to these challenges, biocontrol agents have emerged as a promising alternative for managing phytopathogens. Among these agents, lactic acid bacteria (LAB) have garnered increasing attention in recent years. LAB research offers a new avenue for combatting phytopathogens while addressing concerns related to biosafety and sustainable agricultural practices. This paper aims to provide a comprehensive overview of LAB›s antagonistic capabilities, its role in promoting plant growth, the underlying mechanisms of action, and the limitations it may encounter as a biological control agent (BCA). By shedding light on the advantages of LAB, this review underscores their potential as eco-friendly alternatives to chemical treatments, supporting the sustainable productivity of crops.

**Keywords:** Lactic Acid Bacteria, Plant Growth, Plant Disease Management, Phytopathogens, Biological Control Agent.

## 1. Introduction

The Food and Agriculture Organization (FAO) of the United Nations has projected a formidable challenge for farmers worldwide. To satisfy the needs of an anticipated population surge, estimated at 9.3 billion people by 2050 (UNDP), agricultural output must increase significantly, ranging from 70 to 100 percent more food production [1]. However, this endeavor is complicated by a confluence of factors beyond population growth, including the depletion of natural resources, the specter of climate change, and the emergence of new pests and diseases. Agriculture grapples with substantial economic losses, with pests and diseases alone accounting for 20 to 40 percent of annual economic losses in agricultural products. These adversaries diminish crop yields, compromise quality, and even introduce harmful substances into our food supply [2].

Phytopathogens, responsible for a multitude of plant diseases, cast a pervasive shadow on global crop production, resulting in significant annual losses. Pathogenic agents encompass fungi, bacteria, viruses, protozoa, insects, and parasitic plants. Their presence manifests through various symptoms such as wilting, necrosis or spotting, mold, pustules, rot, hypertrophy or overgrowth, mummification-induced distortion, discoloration or staining, and outright destruction of affected plant tissues [3]. Plant diseases can be effectively managed through a range of approaches, encompassing cultural, physical, chemical, and behavioural practices. Historically, growers have heavily relied on chemical treatments, such as fungicides and bactericides, for over a century.

However, the sustainability of these synthetic chemical solutions is increasingly in question [4]. Their extensive use has led to a host of issues, including the development of resistance in pathogen populations, adverse impacts on human health, the depletion of beneficial soil microorganisms, the

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introduction of harmful residues into the food chain, and a reduction in microbial biodiversity [5]. Recognizing the shortcomings and challenges associated with chemical treatments, efforts to explore alternatives have gained momentum. This shift has been reinforced by the realization that chemical approaches are often suboptimal or restricted by regulations. Additionally, the imperative to meet the growing demand for food safety and quality has elevated the quest for eco-friendly alternatives. The extensive use of agrochemicals can be supplanted by a less hazardous method, thanks to the emergence of microbial biocontrol agents.

The term "biological control" refers to the practice of reducing the prevalence of plant diseases by applying naturally occurring organisms, including beneficial microorganisms, their by-products, or extracts from plants or animals [6]. These agents employ diverse mechanisms of action against target pathogens, including competition, predation, antibiosis, induced host resistance, and the activity of lytic enzymes. In recent decades, extensive research has explored the potential of beneficial microorganisms as biological control agents (BCAs) against plant pathogenic bacteria. Strains from genera such as Pseudomonas, Burkholderia, Streptomyces, Bacillus, and Trichoderma have gained recognition for their antimicrobial capabilities and their synthesis of a wide range of bioactive compounds [7].

Recent years have witnessed a growing interest in the research surrounding lactic acid bacteria (LAB) as a promising class of microorganisms for countering phytopathogens. The utilization of LAB for both plant protection and stimulating plant growth dates back to the 1980s, with notable contributions by Higa and Kinjo [8]. LAB has demonstrated its capacity to produce compounds effective in managing a broad spectrum of bacterial and fungal phytopathogens [9]. Furthermore, its extensive history of use in food processing has enabled researchers to gain insights into its physiological processes and the bioactive substances it generates.

As a result, LAB has earned the generally regarded as safe (GRAS) status, with minimal exceptions, signifying its safe application in the cultivation of edible crops without posing health concerns to humans [10]. This paper aims to provide a comprehensive review of LAB's antagonistic capabilities, its role in promoting plant growth, and the mechanisms underlying its actions as a biological control agent (BCA). Additionally, it will explore the limitations associated with LAB. The overarching goal of this review is to emphasize the valuable contributions of LAB as potential alternatives to chemical interventions, supporting the sustainability of crop productivity.

### 1.1. Lactic Acid Bacteria (LAB): A Diverse Group of Microorganisms

Lactic acid bacteria, often abbreviated as LAB, constitute a heterogeneous group of bacteria characterized by their Gram-positive nature, catalase-negative enzyme activity, nonsporulating behavior, and the ability to thrive in both aerobic and anaerobic conditions. These bacteria take on various shapes, including rod-shaped (bacilli) or spherical (cocci), and they belong to the Lactobacillales order, encompassing six families and thirty-eight genera [11]. One distinguishing feature of LAB is their production of lactic acid (LA) as the primary end product during saccharolytic metabolism [12]. LAB can be categorized into two main groups based on their LA production: homofermentative and heterofermentative strains. Homofermentative LAB convert sugars into lactic acid exclusively, while heterofermentative LAB generate lactic acid, along with ethanol, acetic acid, and carbon dioxide.

Prominent genera within the LAB group include Lactobacillus, Lactococcus, Enterococcus, Streptococcus, Pediococcus, Leuconostoc, Weissella, and Bifidobacterium [13]. In the past, the identification of LAB was a crucial step to understand their properties and ensure their safety for various applications. Traditional approaches relied on phenotypic and chemical characteristics, including carbohydrate fermentation, fermentative pathways (hetero- or homo fermentation), gas production, motility, and spore formation. However, these methods had limitations, particularly when distinguishing closely related strains with similar nutritional requirements. Today, the most reliable method for accurately identifying LAB is through genomic sequencing, which offers precise insights into their genetic makeup and enables a more comprehensive understanding of these versatile microorganisms.

In recent years, molecular biology has significantly evolved, profoundly impacting microbiology and facilitating the use of 16S rDNA gene sequencing techniques to identify bacteria, including lactic acid bacteria (LAB). These conserved genes have exhibited enough variation to serve as excellent phylogenetic markers for distinguishing organisms down to their genus and species levels (Lo and Chong) [7]. Furthermore, the emergence of whole-genome sequencing (WGS) technology has considerably expedited the development and application of LAB resources. WGS provides researchers with a comprehensive insight into the metabolic characteristics, potential beneficial functions, and application directions of LAB strains, based on the information derived from their complete genomes. Additionally, WGS has facilitated more accurate determinations of the genetic evolution and classification of LAB [14].

The inaugural complete LAB genome sequence was documented in 2001 for the species Lactococcus lactis IL1403 [15]. Since then, genomic data for 7,055 LAB species, including Lactobacillus, Lactococcus, Bifidobacterium, and Streptococcus thermophilus, have been submitted to GenBank [16]. This data has provided a thorough understanding of the industrial applications and metabolic characteristics of LAB. WGS has also enabled the assessment of the safety of LAB strains by evaluating genes associated with drug resistance, virulence, and pathogenicity, as well as determining the potential for horizontal gene transfer of these associated genes [17].

Furthermore, genome-scale metabolic models (GSMM) can be constructed from whole-genome data to simulate bacterial behavior in varying environments and systematically guide metabolic engineering efforts. The first GSMM of LAB

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was created using the genome sequence of Lactococcus lactis IL1403, successfully predicting and confirming the minimum medium required for strain development and optimizing metabolism to enhance diacetyl production [18]. Several other successful applications of GSMM in steering microbial improvement and metabolic engineering in LAB have also been documented [19].

### 1.2. Role of Lactic Acid Bacteria in Disease Prevention and Enhancement of Plant Growth

Certain species of lactic acid bacteria (LAB) possess qualities that make them suitable candidates as biological control agents (BCAs), although they may not be as well-known in this role as other groups such as Pseudomonas, Burkholderia, Streptomyces, Bacillus, and Trichoderma. Reports have shown that several LAB species can suppress the activity of phytopathogens and simultaneously encourage plant growth [20]. LAB can play a direct role in plant health by aiding the absorption of crucial nutrients like phosphorus and potassium, facilitating nitrogen fixation, and producing plant hormones and siderophores. Indirectly, LAB can contribute to biocontrol by producing various antimicrobial compounds such as diketopiperazines, hydroxy derivatives of fatty acids, 3-phenyllactate, antibacterial bacteriocins, and bacteriocin-like inhibitory substances (BLIS), as well as organic acids, hydrogen peroxide, pyrrolidone-5-carboxylic acid, diacetyl, and reuterin [21]. These substances can modulate the plant's defense mechanisms, induce systemic resistance, and reduce the availability of iron to pathogens. There is also a possibility that LAB utilizes multiple mechanisms to combat phytopathogens [22].

### 1.3. Indirect mechanisms

### 1.4. Hydrogen Peroxide

Hydrogen peroxide (H2O2) is a type of reactive oxygen species produced by LAB when exposed to oxygen. Its potent oxidizing properties can cause significant damage to the crucial molecular structures of proteins essential for cellular metabolism in microbial cells. This, in turn, hampers the growth of both psychotropic and pathogenic microorganisms. Nevertheless, recent studies suggest that the antimicrobial efficacy of H2O2 might be somewhat limited, given that bacteria tend to produce it in small quantities. Furthermore, its impact is likely to be more pronounced when acting in synergy with other antifungal substances [23].

### 1.5. Organic acid

Organic acids play a crucial role in the antimicrobial activity of LAB, effectively inhibiting a broad spectrum of target microorganisms, as documented in multiple studies [24]. While lactic acid is the predominant metabolite produced by LAB, other acids such as acetic, propionic, formic, benzoic, and PLA are also generated. Lactic acid is known to exert its antibacterial effects by disrupting the membrane functions of pathogens, impeding active transport, lowering intracellular pH, and inhibiting various metabolic activities, ultimately leading to the demise of the target microorganism [25]. However, the production of lactic acid and its associated pH-lowering impact can vary based on the species or strain of LAB, the culture mix, and the conditions under which growth occurs [26]. It is worth noting that many bacteria, fungi, and yeasts are susceptible to the antimicrobial action of lactic acid, particularly its undissociated form at low pH levels, although the extent of their vulnerability can vary significantly.

### 1.6. Reuterin

Some strains of lactobacilli are known to produce the glycerol-derived antimicrobial compound reuterin, and its production can be stimulated directly or indirectly by the presence of glycerol under anaerobic conditions. LAB lack an oxidative pathway to utilize glycerol as their primary carbon source, so they need an alternative carbon source to facilitate glycerol breakdown [27]. Reuterin is a potent inhibitor with a broad spectrum of activity that is independent of pH. It resists degradation by proteolytic and lipolytic enzymes and inhibits DNA replication [28]. Reuterin has shown effectiveness against various fungi, including species of Fusarium, Penicillium, and Aspergillus, and has been associated with preventing mycotoxin development in fermented foods [29]. Additionally, it inhibits the growth of gram-positive and gram-negative bacteria, enteropathogens, yeast, fungi, protozoa, and viruses [30].

### 1.7. Bacteriocin

Bacteriocins, which are ribosomal generated antimicrobial peptides produced by bacteria, can neutralize related or unrelated bacterial strains without harming the bacteria that produce them [31]. They employ various modes of antimicrobial action, such as interfering with cell wall formation, disrupting the cytoplasmic membrane, inhibiting protein synthesis, interrupting DNA replication and transcription, and obstructing septum formation [32]. Certain LAB strains generate bacteriocins and bacteriocin-like inhibitory substances (BLIS). Typically, LAB bacteriocins are either small, heat-stable, or large, heat-labile proteins or protein complexes with antibacterial activity. Importantly, producer cells are immune to their own bacteriocin(s) [33]. Factors like pH, nutritional sources, and incubation temperature significantly influence bacteriocin synthesis. Four main classes of LAB bacteriocins have been identified based on their biochemical and genetic characteristics: lantibiotics (class 1), small, heat-stable non-lanthionine peptides (class 2), large heat-labile proteins (class 3), and complex bacteriocins with lipid and carbohydrate moieties (class 4) [34]. Recent research suggests that bacteriocin-mediated resistance in plants could potentially be harnessed for managing bacterial infections in economically significant crops [35].

### 1.8. Fatty acids

Hydroxy fatty acids (FAs) exhibit antimicrobial properties, as observed by [36]. These acids are prevalent in various organisms, such as mammals and plants. Within bacteria, 3-OH-FAs exist as components of lipopolysaccharides or poly-hydroxyalkanoic acids, although these specific forms have not been identified in LAB. Notably, over 90% of cellular FAs in LAB are saturated and monounsaturated, and these are integral to classifying different LAB strains [37]. Interestingly, some Leuconostoc strains have been found to contain 2-hydroxyhexadecanoic acid and 3-hydroxyheptadecanoic acid. Furthermore, LAB can metabolically convert unsaturated FAs into OH-FAs, suggesting the existence of hydroxylation pathways in LAB [38]. However, the specific function

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of 3-OH-FAs in LAB metabolism remains an open question. A study by Sjögren et al. found that 4-OH-FAs extracted from L [39]. plantarum MiLAB 14 act as detergents, disrupting the cellular membranes of target organisms. Similarly, cis-9-heptadecenoic acid, which resembles 3-OH-FAs, is effective in penetrating the lipid bilayers of fungal membranes. This process ultimately leads to the cytoplasmic disintegration of fungal cells by increasing membrane permeability and causing the release of intracellular electrolytes and proteins.

### 1.9. Cyclic dipeptide

Cyclic dipeptides, or cyclodipeptides (CDPs), also known as 2,5-diketopiperazines, represent the smallest class of cyclic peptides, with bacteria accounting for nearly 90% of their production [40]. Known antimicrobial CDPs extracted from LAB include cyclo (Gly-Leu), cyclo (Phe-Pro), cyclo (Phe-OH-Pro), and cyclo (Leu-Leu) [41]. These cyclic peptides are attractive due to their stability under various environmental conditions, such as pH, heat, and enzyme presence. A specific example of an antifungal CDP is cyclo (Gly-Leu) from Lb. plantarum VTT E-78076, which has demonstrated effectiveness against the plant fungal pathogens Fusarium avenaceum [42]. Despite their promising antimicrobial properties, further research is required to fully comprehend the mode of action and potential applications of these compounds.

### 1.10. Direct mechanisms

Phytohormones production: Both plants and bacteria synthesize phytohormones in minuscule amounts, yet these compounds can significantly influence plant growth by extending root hair length and surface area, thereby enhancing root nutrition and water absorption [43]. These phytohormones also bolster plant defenses, uphold normal cellular functions, and contribute to abiotic stress resistance [44]. Several LAB species are capable of producing phytohormones such as gibberellin (GA) and auxins like indole-3-acetic acid (IAA), which are instrumental in promoting plant growth. For instance, Turaeva et al. identified GA4 and GA7 in the culture fluid of L [21, 45]. plantarum, which were found to enhance the growth and development of wheat coleoptiles, as analyzed through HPLC-MS. However, the specific mechanisms underpinning these processes remain to be fully elucidated.

Regulating Nutrient Absorption and Nitrogen Fixation: Certain strains of LAB play a vital role in enhancing the availability of nutrients from compost and various organic or inorganic sources for plants [21]. Phosphorus (P), a crucial macronutrient for plant growth, is primarily found in soil, either in organic or inorganic precipitated form. Likewise, a shortage of potassium (K), predominantly present in a fixed form, negatively affects plant growth and yield. De Lacerda et al. suggested that the gene sequences encoding for two types of alkaline phosphatase-enzymes that facilitate phosphate mineralization – empower L [46]. lactis to solubilize various phosphorus compounds. The acidity induced by LAB, resulting from the synthesis of organic acids, further aids in the solubilization of P and K, thereby making these elements accessible for plant absorption. In addition to the capacity of LAB to dissolve phosphate, Giassi et al. reported that some LAB strains are also proficient in fixing atmospheric nitrogen for plant utilization [47]. Biological Nitrogen Fixation (BNF) is a process where atmospheric N2 is converted into ammonia and nitrate with the aid of the nitrogenase enzyme complex. Higdon et al. identified that L. lactis strains isolated from the mucilage microbiota of Sierra Mixe maize were diazotrophs, capable of BNF [14]. Proteomic analysis revealed molecular functions related to polysaccharide catabolism, glycan-mediated host adhesion, iron/siderophore utilization, FeMo cofactor biosynthesis (NifB), and novel oxidoreductase activities in the identified unknown genes of L. lactis, underscoring their significance in the BNF trait.

### 1.11. Prospective Influence of LAB on Plant Resilience to Stress

Protection of Plants from Biotic Stress Factors: The prevalence of biotic and abiotic stressors is an increasing threat to crop yields, with the emergence of plant diseases, pests, and the impacts of climate change being more frequent worldwide. LABs have demonstrated their capacity to enhance crop development and yield by instilling tolerance to various stressors. These bacteria exhibit a myriad of functional attributes and can colonize plant tissues, thereby contributing positively to plant growth and survival. There have been numerous investigations into the efficacy of LAB in mitigating the effects of bacterial and fungal phytopathogens on crops (Table 1).

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**Table 1: Selected lactic acid bacteria with biological control and bio stimulant propertie.**

| Strain | Source | Pathogen/Crop | Mechanism/Effect | References |
|---|---|---|---|---|
| **(i) Biocontrol** | | | | |
| Lactobacillus | | | | |
| plantarum | Cucumber pickle | Pseudomonas campestris, Ralstonia solanacearum, Xanthomonas campestris pv. vesicatoria, Pectobacterium carotovorum | Organic acids | Visser et al., 1986 |
| Lactobacillus sp. | Tomato rhizosphere | Ralstonia solanacearum, Xanthomonas axonopodis pv. citri, X. campestris pv. vesicatoria, Erwinia pyrifoliae, Pectobacterium carotovorum | None | Shrestha et al., 2009a;<br>Shrestha et al., 2009b |
| Lactobacillus plantarum | Kimchi | Aspergillus flavus | 3,6-bis (2 methylpropyl)-2,5 piperazinedion | Yang & Chang, 2010 |
| Lactobacillus sp. | Dairy products | Fusarium oxysporum | SAR, antifungal metabolites | Hamed et al., 2011 |
| Lactobacillus plantarum | Fermented mare milk | Botrytis cinerea, Alternaria solani, Phytophthora drechsleri, Fusarium oxysporum and Glomerella cingulate | Proteinaceous and non-proteinaceous antifungal Compounds | Wang et al., 2011 |
| L. fermentum | Fermented food, dairy products | A. niger, Fusarium graminearum, A. oryzae | Proteinaceous, PLA | Muhialdin et al., 2011;<br>Gerez et al., 2013 |
| Lactobacillus plantarum | Durian fruit | Colletotrichum capsici, broad spectrum | Unknown | El-Mabrok et al., 2012 |
| Lactobacillus plantarum | Ginger root | Colletotrichum capsici, broad spectrum | Unknown | El-Mabrok et al., 2012 |
| Lactobacillus paracasei | Tomato, soil | Ralstonia solanacearum | Unknown | Murthy et al., 2012 |
| W. paramesenteroides | Fermented wax gourd | Rhizopus stolonifera, Sclerotium oryzae, Rhizoctonia solani, Botrytis cinerea, Sclerotinia minor, Rhodotorula sp | Organic acids | Lan et al., 2012;<br>Sathe et al., 2007 |
| Lactobacillus acidophilus | Chicken intestine | Fusarium sp., Alternaria alternata, P. paneum, Cladosporium sp., Rhizopus oryzae | Organic acids | Oliveira et al., 2014;<br>Schnürer and Magnusson, 2005 |
| Lactobacillus Paracasei | Tomato, soil | Ralstonia solanacearum | SAR | Konappa et al., 2016 |
| Weisella cibaria, Lactococcus lactis subsp. Lactis | Papaya seed | Erwinia mallotivora | Organic acids, hydrogen peroxide | Taha et al., 2019 |
| L. pentosus | Fruit, fermented food | A. oryzae, A. niger, Fusarium sp. | PLA | Ouiddir et al., 2019 |
| Lactobacillus pentosus, Leuconostoc fallax | Fermented vegetables | Alternaria brassicicola, Xanthomonas campestris pv. campestris, Pectobacterium caratovorum | Unknown | Lin et al., 2020 |
| Lactobacillus Plantarum | Yellow pithaya | Fusarium fujikuroi | Unknown | Valencia- Hernandez et al., 2021 |
| Lactobacillus acidophilus | Mango | C. gloeosporioides | Antifungal compound, lytic enzyme | Ranjith et al., 2021 |
| Lactiplantibacillus plantarum | Collection of Pure Cultures of Industrial Microorganisms ŁOCK at the Lodz University of Technology, pickled vegetables, milk | Pectobacterium carotovorum, Streptomyces scabiei, Alternaria solani, Alternaria tenuissima, Alternaria alternata, Phoma exigua, Rhizoctonia solani, Colletotrichum coccodes | Organic acids | Steglińska et al., 2022 |

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|---|---|---|---|---|
| Lactobacillus sp. | Rhizosphere soil of tomato | Pepper | IAA, phosphate solubilization, and biocontrol property Increased root and shoot length, root fresh weight and chlorophyll content | Steglińska et al., 2022 |
| Enterococcus faecium | Rhizosphere soil of oriental melon (Cucumis melo L.) | Rice | Phytohormones (GA, IAA), mineral solubilization, and biocontrol property-Increased shoot and root length, plant fresh weight, chlorophyll content, nutrient uptake | Lee et al., 2015 |
| L. plantarum | PGPR Corp. (Korea) | Cucumber | Succinic acid, lactic acid increased growth, nutrient availability and amino acid content | Kang et al., 2015 |
| Lactobacillus sp. | Sugarcane fermentation | Citrus seedling | Nitrogen fixation, phosphate solubilization increased height, stem diameter, root and shoot weight | Giassi et al., 2016 |
| Enterococcus sp. | Rhizosphere soil of grass pea | Fusarium oxysporum f. sp. lentis | IAA, phosphate solubilization, stress response and biocontrol property | Mussa et al., 2018 |
| E. faecium LB5, L. lactis LB6, LB7, and LB9 | Rhizosphere soil of wheat | Fusarium graminearum | Phosphate solubilization and biocontrol property | Strafella et al., 2021 |
| Lactobacillus sp. | Vietnamese traditional Nem chua | Peanut seed | IAA, phosphate solubilization, and biofilm formation -Increased seed germination, vigor index, plant length, and total fresh weight | Nguyen et al., 2021 |
| Lactobacillus sp. | Silage and rhizosphere soil | Adzuki bean (Vigna angularis), Arabidopsis | 3-phenyllactic acid (PLA) -Root promoting activity in Adzuki bean, promote auxin signaling pathway – increased lateral root density in Arabidopsis | Maki et al., 2021, 2022 |
| Weisella cibaria, | | | | |
| Lactococcus lactis subsp. lactis | Papaya seed | Papaya | Synthesis of ammonia, siderophores, and phosphate solubilization -increased the dry weight of the shoot and root of papaya plants | Jaini et al., 2022 |
| Lactobacillus sp. | The aerial part of pomegranate plants | Fusarium sp. | Phytohormones (GA, IAA) and biocontrol property | Abhyankar et al., 2022 |

For example, in vitro and in planta assays were utilized to screen Lactobacillus plantarum and Leuconostoc mesenteroides strains against three bacterial pathogens affecting kiwifruit (Pseudomonas syringae), Prunus (Xanthomonas arboricola), and strawberry (Xanthomonas fragariae) (Daranas et al.,). These strains were selected for their broad-spectrum preventive activity against all three pathogens. Furthermore, the biocontrol performance of L. plantarum strains was comparable to reference controls in both semi-field and field studies. The generation of lactic acid and a subsequent decrease in pH were identified as partial contributors to the inhibitory mechanism observed in vitro. Additionally, both strains exhibited similar survival rates when applied to leaf surfaces.

A similar broad-spectrum inhibition was reported for the species L. paracasei and L. plantarum isolated from wine fermentations [48]. These LAB strains not only inhibited various

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food spoilage Gram-positive bacteria but also demonstrated a 55-76% efficacy in preventing the growth of Fusarium oxysporum sp. lycopersici, a phytopathogenic fungus that affects tomatoes, in vitro. This efficacy was competitive when compared to previous studies of L. plantarum isolated from different sources [49]. Furthermore, plant-derived Weissella confusa and Pediococcus pentosaceous strains exhibited a broad-range inhibitory action against fungal diseases affecting fruit crops [50].

Steglińska et al. conducted a screening of LAB against ten phytopathogens related to potato, including Pectobacterium carotovorum, Fusarium oxysporum, and Rhizoctonia solani [51]. The results revealed a 40-90% reduction in disease, except for Fusarium oxysporum and Fusarium sambucinum, which were not inhibited by Lactiplantibacillus plantarum KB2 LAB 03. The metabolic profile analysis of the LAB strains identified abundant compounds from organic acids and ethanol. Zebboudj et al. reported that L [52].

lactis subsp. diacetylactis could inhibit Fusarium species responsible for tomato crown and root rot by up to 62.42% on MRS agar medium. Similarly, Valencia-Hernandez et al. found that a biomass fraction of Lactobacillus plantarum isolated from yellow pitaya inhibited Fusarium fujikuroi growth by 100% over 48 hours of fermentation. Lin et al. observed that Lactobacillus pentosus and Leuconostoc fallax, sourced from fermented vegetables, combined with chitosan, effectively inhibited three cruciferous vegetable diseases: cabbage black spot caused by Alternaria brassicicola, black rot caused by Xanthomonas campestris, and soft rot caused by Pectobacterium carotovorum [53, 54].

Moreover, the LAB/chitosan mixture also showed antagonistic effects against Colletotrichum higginsianum, Sclerotium rolfsii, and Fusarium oxysporum f. rapae, showcasing a broad-spectrum activity. Notably, multiple applications of the treatment proved more successful than a single application. A significant reduction in the severity of papaya dieback disease was observed following the application of the LAB combination Weisella cibaria and Lactococcus lactis in nurseries [55]. In addition, Lactobacillus acidophilus, isolated from mango (Mangifera indica L.), demonstrated more than 40% inhibitory action against post-harvest anthracnose caused by C. gloeosporioides. In vitro evaluations revealed that the isolates produced antifungal chemicals and lytic enzymes as mechanisms of antagonism against the fungus [56].

Lactic Acid Bacteria (LAB) has been found to possess a range of properties that stimulate the growth of plants, enhancing nutrient availability to the host plants. This enables plants to handle stress and combat plant nematodes effectively [57]. Strafella et al. demonstrated that sixteen strains of LAB were capable of solubilizing significant amounts of phosphate. These findings are in line with those of Mussa et al., who isolated similar strains from the Enterococcus sp [58]. LAB can directly promote plant growth by increasing the uptake of minerals and nutrients or indirectly by modulating plant hormones like indole-3-acetic acid (IAA), cytokinin, and ethylene. Mohite found that LAB produces IAA, a plant hormone that stimulates rapid plant growth [59]. Abhyankar et al. identified three isolates from the aerial parts of the pomegranate plant as Leuconostoc sp. and Lactobacillus sp [60]. These isolates displayed antifungal activity against Fusarium sp. and also exhibited 1-Aminocyclopropane 1-carboxylic acid (ACC) deaminase activity, which is crucial for reducing ethylene to non-toxic levels, thereby protecting the plants. The isolate GYP3 was found to produce IAA and Gibberellin, both of which support root elongation and flowering. Furthermore, all three isolates produced Exopolysaccharide (EPS). A study by Lee et al. examined the plant growth-promoting capacity of Enterococcus faecium LKE12, a LAB strain from the rhizosphere of the oriental melon (Cucumis melo L.) [61].

This strain was tested on a gibberellin (GA)-deficient rice dwarf mutant (waito-C) and a normal GA biosynthetic rice cultivar (Hwayongbyeo). The results showed that both rice cultivars significantly benefited from E. faecium LKE12's secretion of various GAs and IAA, which increased the shoot length and biomass of the plants. Nguyen et al. isolated Lactobacillus spp [62]. L5, L3, and L2N from traditional Vietnamese Nem chua. These isolates were found to synthesize IAA, solubilize phosphate, and develop biofilms. Treating peanut seeds with these bacterial cultures improved seed germination and vigor index compared to untreated seeds and those treated with fungicides.

The treated seeds also displayed a 22.4% increase in height and a 99.6% increase in total fresh weight. Shrestha et al. found that in greenhouse and field evaluations, LAB strains KLF01 and KPD03 outperformed LAB strain KLC02 in terms of growth promotion due to their ability to secrete significant amounts of IAA. However, in field tests, KLC02 outperformed KLF01 and KPD03 [63]. This variation in results could be attributed to environmental conditions, root colonization, competition, and the synthesis of antagonistic metabolites. Lutz et al. also observed growth-promoting effects of several other LABs on cucumber and tomato seedlings [64].

Effective Microorganisms (EM) consortiums are composed of a diverse range of microorganisms, including yeast, mold fungi, lactic acid bacteria (LAB), photosynthetic bacteria, actinomycetes, and more. The integration of EM into compost has proven to enhance crop yields and nutrient absorption, as demonstrated in various studies [21]. Lactic acid bacteria-based fermented compost products have been shown to improve soil fertility, structure, and aeration, neutralize soil alkalinity, and boost moisture retention. A traditional Japanese fertilizer known as Bokashi is a prime example of EM-enriched compost. Maki et al. identified a root-stimulating compound, 3-phenyllactic acid (PLA), in Bokashi fertilizer [65].

PLA is an essential organic acid produced by various bacteria, predominantly LAB, as a result of phenylalanine catabolism through phenylpyruvic acid (PPA). It has been established as biologically active in promoting plant root growth. A subsequent study by Maki et al. revealed that PLA stimulates the auxin signaling system, subsequently affecting root

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development in Arabidopsis [66]. PLA was found to increase lateral root density while reducing primary root growth in Arabidopsis, also elevating the expression of the auxin response marker gene IAA19 in the roots. This auxin-like activity of PLA was significantly diminished in the auxin signaling mutant, tir1-1 afb2, suggesting that PLA regulates root development via the auxin signaling pathway. In an experimental study conducted by Javaid, the addition of lactic acid bacteria to farmyard manure significantly enhanced the root and shoot growth of rice (Oryza sativa L.), although the same results were not observed in NPK-amended soil.

Somers et al. also discovered that Lactococcus lactis, isolated from organic soil, facilitated plant growth in cabbage [67]. Contrary to previous beliefs that LAB requires minimal iron (Fe) and does not produce siderophores, genome analysis of two vegetable-isolated Lactococcus lactis strains by Shrestha et al. revealed non-ribosomal peptide pathways, indicating LAB's potential to produce siderophores [63]. Further investigation by Jaini et al. uncovered the synthesis of ammonia and siderophores, along with phosphate solubilization, which led to an increase in the dry weight of both the shoot and root of papaya plants, as reported in the study by Taha et al. [20, 55].

Mitigating Abiotic Stress in Plants: Various abiotic stressors, such as drought, extreme temperatures, high salinity, presence of toxic metals, and exposure to organic pollutants, can significantly hinder plant growth. When subjected to these stressors, plants may experience a disruption in their intracellular redox balance, leading to the production of reactive oxygen species (ROS). The plant then activates its enzymatic and non-enzymatic antioxidant defenses to counteract the damaging effects of ROS. During drought or dehydration, plants increase the biosynthesis of nitric oxide (NO) as a means to mitigate oxidative stress. A study conducted by Yarullina et al. demonstrated that root treatment of wheat seedlings with Lactobacillus plantarum 8P-A3 helped alleviate oxidative stress caused by dehydration.

This was evidenced by increases in total integral antioxidant capacity (IAC) and catalase activity, suggesting that NO plays a crucial role in the stress-limiting functions of lactobacilli by diminishing the harmful effects of dehydration [68]. High salt levels in soil can result in ion imbalance and toxicity for plants. In response, plants may produce polyamines and osmolytes, activate defense mechanisms, inhibit the accumulation of reactive oxygen species, and regulate ion transfer to combat salinity stress. Research by Phoboo et al. revealed that Swertia chirayita plants inoculated with Lactobacillus plantarum exhibited enhanced tolerance to salinity stress [69]. This was attributed to the plants' adoption of more energy-efficient defense strategies and effective partitioning of carbon flow between primary and secondary metabolism. Although the intricacies of plant stress response networks are not fully comprehended, it has been observed that treatment with LAB can improve plants' ability to cope with stress.

### 1.12. Barriers, Obstacles, and Future Directions

Similar to other biological control agents (BCAs), LAB faces its own set of limitations and challenges in practical applications. A notable gap exists in the evidence connecting LAB's antagonistic effects observed in vitro to actual pathogen control in field conditions. The primary limitation in utilizing LAB, and other BCAs, in agriculture is their ability to survive and produce ample bioactive compounds under optimal conditions. To overcome these limitations, one approach is to select or genetically engineer strains that can thrive in the Phyto microbiome. This can be achieved by supplementing cultures with the necessary nutrients or protective carriers, and reapplying cultures to maintain a high number of viable cells.

However, these methods are complex and time-consuming. An alternative approach is to utilize biotechnology to develop transgenic strains with diverse modes of action. These improved strains could possess desirable characteristics such as ease of formulation, stability, and an enhanced ability to colonize plants. Another potential strategy is to utilize a LAB strain more frequently in environments conducive to its growth, such as fruits, flowers, and organic-rich soils. This approach has shown efficacy in preventing and eradicating floral diseases in rosaceous tree crops and has demonstrated promising results against postharvest infections as well [70, 71].

The synthesis of bioactive substances can be effectively achieved by cultivating Lactic Acid Bacteria (LAB) in bioreactors under optimal conditions. Previous research by Limanska et al. has established that LAB's metabolites are crucial to their bioactivity, and the extraction and purification of these metabolites has been successfully implemented [65, 72, 73]. While LAB can tolerate a range of environmental stresses, they require specific nutrients to thrive. Investigations have been conducted on utilizing waste from sugar beet and sweet potato processing as industrial LAB media, yet a more stable LAB medium is necessary for prolonged industrial culture [74].

Caution is also necessary when establishing mixed consortia of LAB with other Plant Growth-Promoting Microbes (PGPM) to avoid incompatibility. Nanotechnology, having made significant contributions to the fields of energy, medicine, and electronics, is now finding its place in agriculture [75]. Successful applications of metal nanoparticles (M-NPs) such as silver (Ag), iron (Fe), copper (Cu), zinc (Zn), and selenium (Se) have been documented in suppressing various phytopathogens and promoting plant growth in agriculture [76]. However, the chemical and physical methods used to produce M-NPs can be expensive and potentially harmful to human health and the environment. In response, green synthesis has emerged as a leading approach in this field, exploring the potential of microorganisms and plants as nanofactories.

Green synthesis of M-NPs offers numerous advantages including environmental friendliness, cost-effectiveness, non-toxicity, speed, reliability, stability, sustainability, low polydispersity, scalability, and biocompatibility. Recent studies have highlighted the potential nanobiotechnological ap-

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plications of LAB in the synthesis of both intracellular and extracellular M-NPs, laying the groundwork for further exploration into the role of this bacterial group in supporting plant growth and controlling phytopathogens [77]. While LAB is generally recognized as safe (GRAS) and has a long history of safe usage, it is essential to ensure the safety of the selected LAB.

Strains before their industrial application to prevent potential impacts on ecosystem biodiversity or risk of diseases in humans, animals, or plants. For instance, Linares-Morales et al. reported promising results of E [78]. faecium against post-harvest pathogens, but further assessment of the strains' safety is necessary due to the potential presence of harmful genes in some Enterococcus strains [79]. The advancements in genome analysis over the past decade have facilitated the safety screening of LAB strains by evaluating genes related to drug resistance, virulence, and pathogenicity, as well as determining the potential for horizontal gene transfer [17].

## 2. Conclusion

LAB strains have demonstrated their capability to enhance crop production through various mechanisms, such as acting as biological control agents (BCAs), improving nutrient availability, mitigating the impact of biotic and abiotic stressors, and directly promoting plant growth. Given their generally recognized as safe (GRAS) status and extensive research background in food science, LAB strains are well-suited for applications in crop protection. Although LAB strains are commonly found in the phytomicrobiome, their potential as BCAs and contributors to plant development have often been overlooked. Historical and current evidence suggests that LAB strains have the potential to serve as sustainable and safe agricultural inputs, assisting in the control of plant diseases and the enhancement of plant growth. Future research on LAB strains should focus on their biocontrol efficiency in field conditions, as well as their bioproduction and formulation processes. Integrating LAB strains as BCAs within comprehensive control programs that employ multiple biocontrol strategies could prove to be an effective approach in enhancing resistance against phytopathogens and addressing the challenges of achieving sustainable food security [80.

## Acknowledgements

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