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A review on the antimicrobial activity of *Lactiplantibacillus plantarum* metabolites

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Abstract: The increasing demand for natural alternatives to chemical preservatives and antibiotics has intensified interest in probiotic microorganisms with intrinsic antimicrobial properties. *Lactiplantibacillus plantarum*, a well-characterised species within the family *Lactobacillaceae*, is widely recognised for its broad-spectrum antibacterial activity and its long history of safe use in fermented foods. This review provides a comprehensive synthesis of recent advances in the antimicrobial functionality of *L. plantarum*, covering its taxonomic classification, genomic features, and the diverse array of antimicrobial metabolites it produces, including bacteriocins, organic acids, hydrogen peroxide, lysozyme, siderophores, and short-chain fatty acids (SCFAs). The mechanisms of action of these compounds, strain-specific variability in antimicrobial efficacy, the role of biofilm formation, and synergistic interactions among different metabolites are discussed in detail. Key application domains, such as food preservation, medical therapy, and agricultural biocontrol, are critically evaluated. The primary objective of this review is to systematically consolidate current knowledge, identify core scientific questions and technical bottlenecks, and provide a theoretical foundation for the development of safe and effective natural antimicrobial agents based on *L. plantarum*. Furthermore, the review outlines strategies to bridge the gap between laboratory research and industrial implementation, thereby facilitating the translation of this probiotic into practical applications.

Keywords: bacteriocins; natural alternatives; probiotics; strain-specific efficacy; synergistic inhibition

INTRODUCTION

With the escalating crisis of antibiotic-resistant bacteria caused by global antibiotic misuse, traditional antimicrobial approaches are facing severe challenges. According to the World Health Organisation (WHO), the annual death toll from infections caused by antibiotic-resistant bacteria has exceeded 1 million, and this figure is projected to soar to 10 million by 2050 (Nazir et al. 2025),

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posing a direct threat to global public health security. Concurrently, the widespread use of chemical preservatives in the food industry has raised consumer concerns regarding food safety, creating an urgent global demand for natural and safe antimicrobial alternatives in both scientific research and industrial sectors (El Alami El Hassani et al. 2025). In this context, exploring microbial resources with the broad-spectrum antimicrobial activity and low propensity to induce resistance has emerged as a critical pathway to address the challenges of antibiotic-resistant bacteria and food preservation.

Probiotics as a class of live microorganisms capable of colonising the host, improving microbial balance, and providing clear health benefits, have attracted considerable interest in recent years (Guo et al. 2025). As outlined by the International Scientific Association for Probiotics and Prebiotics (ISAPP), probiotics must satisfy the four fundamental criteria: adequate viability at the time of administration, strain-level identification, scientifically substantiated health benefits, and a documented history of safe use (Tomicic et al. 2025). A growing body of evidence has demonstrated the diverse health-promoting effects of probiotics, including the regulation of intestinal microbial equilibrium, reinforcement of the gut epithelial barrier, inhibition of pathogenic bacterial colonisation, and immunomodulatory activity (Mauriello et al. 2025). Currently, commercially available probiotic products are predominantly derived from lactic acid bacteria (particularly species of *Lactobacillus* and *Bifidobacterium*) and spore-forming *Bacillus* species. Among these, *Lactobacillus* species occupy a dominant position in the global probiotic market, owing to their high tolerance to gastric acid and bile salts, robust intestinal colonisation capacity, and the production of diverse bioactive metabolites (Augustynowicz et al. 2025). *Lactiplantibacillus plantarum* (formerly *Lactobacillus plantarum*) is recognised as one of the most extensively characterised probiotic species within the genus *Lactobacillus*. Its antimicrobial properties have demonstrated a considerable application potential across multiple domains, including food preservation, healthcare, and agricultural biocontrol (Hosseinzadeh et al. 2026). In recent years, amid the escalating challenge of antibiotic resistance and the growing recognition of the limitations associated with conventional antibiotics, *L. plantarum* has attracted growing interest as a potential alternative to chemical preservatives and antibiotics. This interest is largely attributable to its natural origin, favourable safety profile, and low propensity to induce microbial resistance. The antibacterial mechanisms of *L. plantarum* are multifaceted. The secondary metabolites it produces, including organic acids (e.g. lactic acid), hydrogen peroxide, bacteriocins, and biosurfactants, exert their antimicrobial effects by disrupting the integrity of pathogenic bacterial cell membranes, interfering with energy metabolism, and inducing oxidative stress (Echegaray et al. 2023).

Although considerable progress has been made in understanding the antimicrobial functions of *L. plantarum*, the majority of studies have predominantly focused on individual strains or confined application contexts. As a result, a comprehensive synthesis of its mechanisms of action, strain-specific variability, and a cross-sectoral application potential remain missing. Therefore, the present review aims to systematically synthesise recent advancements in the antibacterial properties of *L. plantarum*, with a particular focus on elucidating its taxonomic classification and genomic features, characterising the strain-specific diversity in antimicrobial efficacy, detailing the mechanistic roles of its metabolites, and critically evaluating its innovative applications in food preservation, medical therapy, and agricultural biocontrol. By systematically addressing these core scientific questions and associated technical challenges, this review seeks to establish a theoretical foundation for the development of effective and safe natural antimicrobial agents, while also outlining practical pathways to facilitate the translation of *L. plantarum*-based strategies from laboratory research toward industrial application.

BIOLOGICAL CHARACTERISTICS AND ANTIMICROBIAL POTENTIAL OF *L. PLANTARUM*

Classification and distribution of *L. plantarum*

L. plantarum is a Gram-positive, facultative anaerobic, non-spore-forming rod-shaped bacterium belonging to the family *Lactobacillaceae* and the genus *Lactobacillus* (Seddik et al. 2017). Phylogenetic

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analysis based on 16S rRNA gene sequences has revealed that *L. plantarum* shares over 99% sequence homology with *Lactobacillus pentosus* and *Lactobacillus paraplantarum*, with all three species collectively classified within the *L. plantarum* group (Huang et al. 2017). This species is ubiquitously distributed across diverse ecological niches, including fermented foods (e.g. kimchi, yogurt, and cheese), the human gastrointestinal tract, the oral cavity, and various natural environments (Garcia-Gonzalez et al. 2022). Notably, its population density in kimchi can reach up to 10^8 CFU/g, while it constitutes approximately 5% to 10% of the total lactobacilli residing in the human gut (Jiang et al. 2016). *L. plantarum* exhibits remarkable environmental adaptability, with the capacity to proliferate across a broad range of pH conditions (3.0–9.0) and temperatures (10–45 °C), as well as tolerance to bile salt concentrations up to 0.3% (Yilmaz et al. 2022; Zhang et al. 2025b). For instance, the strain *L. plantarum* WLPL04 has been shown to retain a survival rate of 95% following 3 h of exposure to pH 2.5, and 90% viability after 12 h of treatment with 0.45% bile salts (Jiang et al. 2016).

Genomic characteristics of *L. plantarum*

The genomic architecture of *L. plantarum* is characterised by a genome size ranging from approximately 3.3 Mb to 3.5 Mb, with a GC content of around 44%, encoding an estimated 3 000 genes (van den Nieuwboer et al. 2016). The genome exhibits considerable plasticity, harbouring multiple mobile genetic elements, including plasmids and transposons that facilitate rapid adaptation to diverse environmental niches (Salvetti and O'Toole 2017). For example, the complete genome sequence of *L. plantarum* WCFS1 contains 19 plasmids, several of which carry genes involved in bacteriocin biosynthesis (Siezen et al. 2012; van den Nieuwboer et al. 2016). Similarly, the genome of *L. plantarum* ZDY2013 harbours a 20 kb gene cluster dedicated to the biosynthesis of plantaricin, comprising structural genes, immunity determinants, and transport-related components (Zhang et al. 2016). Moreover, *L. plantarum* strains typically possess an extensive repertoire of genes encoding carbohydrate-metabolising enzymes, enabling the utilisation of a wide range of carbon sources, including glucose, fructose, and maltose (Hu et al. 2025). Notably, *L. plantarum* A6 has been shown to carry genes encoding α-amylase and saccharifying enzymes, conferring the ability to hydrolyse starch into fermentable glucose units (Li and Bi 2025).

Biological functions of *L. plantarum*

L. plantarum demonstrates a broad spectrum of metabolic capabilities, utilising various carbohydrates to generate organic acids, primarily lactic, acetic, and propionic acids, as well as an array of functional metabolites, including bacteriocins and exopolysaccharides (EPS) (Paventi et al. 2024). Among these, lactic acid constitutes the primary metabolic end product, accounting for approximately 70–90% of the total organic acid production (Jang et al. 2023; Popova-Krumova et al. 2024). These metabolic activities are underpinned by key carbohydrate metabolism pathways encoded within the *L. plantarum* genome, including the complete glycolytic pathway, the pentose phosphate pathway, and components of the tricarboxylic acid cycle (Cui et al. 2021). Moreover, certain strains possess the ability to synthesise vitamins such as thiamine (B1), riboflavin (B2), and pyridoxine (B6) (Yin et al. 2024; Keyvan et al. 2025). For example, *L. plantarum* A6 has been reported to produce folate at yields of up to 10 μg/l (Tamene et al. 2023). In addition, metabolites derived from *L. plantarum* exhibit antioxidant properties; for instance, EPS produced by this species have demonstrated 1,1-diphenyl-2-picrylhydrazyl (DPPH) radical scavenging activity reaching approximately 60% (Elmansy et al. 2022).

Beyond its metabolic functions, *L. plantarum* exerts significant immunomodulatory effects by interacting with host immune cells and modulating cytokine production. For instance, *L. plantarum* CRL1506 has been shown to stimulate porcine intestinal epithelial cells to produce type I interferons [e.g. interferon-alpha (IFN-α) and -beta (IFN-β)], resulting in the two- to three-fold upregulation of antiviral effector genes such as MX Dynamin Like GTPase 2 (*MX2*) and 2'-5'-Oligoadenylate Synthetase 1 (*OAS1*) (Mizuno et al. 2020). Similarly, administration of *L. plantarum* P8 in stressed murine models was associated with reduced cortisol levels and increased interleukin-10 (IL-10) concentrations (Khan et al. 2022). These immunomodulatory capacities are closely linked to structural components of the bacterial cell wall. Peptidoglycan,

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in particular, is known to activate Toll-like receptor 2 (TLR2) signalling, thereby stimulating macrophages to produce pro-inflammatory cytokines such as tumour necrosis factor-alpha (TNF-α) and interleukin-6 (IL-6) (Yin et al. 2023). Additionally, *L. plantarum* contributes to immune homeostasis indirectly by modulating the composition of the gut microbiota, promoting the proliferation of beneficial genera such as *Bifidobacterium* while suppressing potentially pathogenic microorganisms like *E. coli*, thereby attenuating intestinal inflammation (Zeng et al. 2023).

The antimicrobial activity of *L. plantarum*

The antimicrobial activity of probiotics constitutes a core functional attribute, mediated primarily through three interrelated mechanisms: the secretion of antimicrobial compounds, including bacteriocins, organic acids, hydrogen peroxide, and lysozyme; competitive exclusion of pathogens by limiting access to nutrients and adhesion sites; and modulation of host immune responses to enhance pathogen clearance (Mariom et al. 2025). Among these, bacteriocins, ribosomally synthesised antimicrobial peptides produced by probiotics, have attracted particular interest due to their broad-spectrum activity, thermostability, and low residue profiles, positioning them as promising alternatives to conventional antibiotics (Simons et al. 2020).

The clinical relevance of probiotic-mediated antimicrobial effects is increasingly recognised. In the management of *Clostridium difficile* infection, probiotic administration aids in restoring the gut microbial homeostasis, with reported reductions in recurrence rates of up to 40% (Yu et al. 2025). Similarly, in bacterial vaginosis, intravaginal application of *Lactobacillus* preparations has been shown to restore physiological pH and achieve cure rates approaching 75% (Udjianto et al. 2025). Moreover, emerging evidence suggests that probiotics may exert synergistic effects when co-administered with antibiotics, enhancing antimicrobial efficacy while permitting a dose reduction. For example, supplementation of probiotics in combination with amoxicillin has been associated with a 15% increase in *Helicobacter pylori* eradication rates (Beikmohammadi et al. 2026).

L. plantarum, as a well-recognised probiotic, produces a diverse array of antimicrobial compounds, including bacteriocins, organic acids, hydrogen peroxide, and lysozyme that collectively contribute to its broad-spectrum antibacterial activity (Echegaray et al. 2023). Among these, bacteriocins such as plantaricin and lactobacillin are recognised as the primary mediators of antimicrobial effects, particularly against Gram-positive bacteria and they select Gram-negative pathogens (Sugrue et al. 2024). For instance, bacteriocins derived from *L. plantarum* KLDS1.0391 have been shown to inhibit the growth of *Listeria monocytogenes*, *Staphylococcus aureus*, and *E. coli* (Goel and Halami 2023). Similarly, *L. plantarum* NC8 produces bacteriocins active against enteropathogens including *Salmonella* spp. and *Shigella* spp. (Pu et al. 2022). Organic acids, notably lactic acid and acetic acid, constitute another major class of antimicrobial metabolites. These compounds exert their inhibitory effects primarily through acidification of the surrounding environment, thereby suppressing the growth of acid-sensitive pathogens (Ibrahim et al. 2021). For example, organic acids secreted by *L. plantarum* I62 have been demonstrated to reduce the viability of *Salmonella* by up to 90% (Hu et al. 2019). In addition, *L. plantarum* produces hydrogen peroxide and lysozyme, which further augment its antimicrobial capacity. Hydrogen peroxide, in particular, exerts bactericidal effects through oxidative damage; it has been reported to reduce the survival of *S. aureus* by approximately 80% (Chen et al. 2023b).

The antibacterial efficacy of *L. plantarum* has been robustly validated through a range of *in vitro* experimental models, including the agar well diffusion assay, broth microdilution method, and epithelial cell adhesion inhibition assays. For instance, *L. plantarum* WLPL04 has been shown to produce an inhibition zone of up to 15 mm against enteropathogenic *E. coli* O157:H7 (Liu et al. 2017). Quantitative assessment using the broth microdilution method revealed that *L. plantarum* HK01 exhibits a minimum inhibitory concentration (MIC) of 0.5 mg/ml against *S. aureus* (Sharafi et al. 2013; Li et al. 2023b). Furthermore, in cell-based adhesion inhibition assays, *L. plantarum* I62 reduced the adherence of *Salmonella* to Caco-2 intestinal epithelial cells by 75% (Cobur et al. 2026). Notably, the antimicrobial potency of *L. plantarum* is strain-dependent. For example, *L. plantarum* 106 demonstrated superior

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inhibitory activity against *E. coli* O157:H7 compared to *L. plantarum* 105 under identical experimental conditions (Baillo et al. 2026). In addition, antibacterial activity varies with the bacterial growth phase; maximum efficacy is typically observed during the logarithmic growth phase, followed by a gradual decline as cells enter the stationary phase (Li et al. 2025a). These findings underscore the importance of strain selection and physiological state in optimising the antimicrobial applications of *L. plantarum*. A summary of antimicrobial activity of *L. plantarum* is presented in Table 1.

The antibacterial mechanism of *L. plantarum*

The antimicrobial activity of *L. plantarum* does not arise from a single factor but is mediated by a combination of metabolic products and cell-associated structures. These components can act independently or synergistically to enhance inhibitory effects against pathogenic microorganisms. Previous studies have shown that this bacterium produces a wide range of bioactive substances, including bacteriocins, organic acids, hydrogen peroxide, lysozyme, siderophores, short-chain fatty acids (SCFAs), EPS, and volatile organic compounds (VOCs) (Echegaray et al. 2023; Hosseinzadeh et al. 2026). These substances exert antimicrobial effects through diverse mechanisms, such as disrupting the cell membrane integrity, interfering with energy metabolism, inhibiting macromolecular synthesis, and competing for essential nutrients. In addition, the ability of *L. plantarum* to form biofilms plays a significant role in its antimicrobial activity by promoting the stable colonisation in the host or environment and enhancing antagonistic effects.

To systematically summarise the functional characteristics of these antimicrobial factors, their primary mechanisms of action, molecular targets, and representative experimental data for different classes of antimicrobial substances are compiled in Table 2 and 3, thereby facilitating a comprehensive comparison of their functional features and potential synergistic interactions. The following sections provide detailed discussions of these components, with particular emphasis on their molecular mechanisms, structural characteristics, and synergistic roles in the overall antimicrobial effect.

Table 1. Antimicrobial activity of *L. plantarum*

Microbial classification	Representative target pathogens	Specific antimicrobial effect	Core active substances	Key influence factors
Gram-positive pathogenic bacteria	*S. aureus*, *L. monocytogenes*, *B. cereus*, *Enterococcus faecalis*	dose-dependent bacteriostatic and bactericidal effects; significantly inhibits bacterial colony growth and biofilm formation	lactic acid, bacteriocins, hydrogen peroxide, short-chain fatty acids	strain specificity, fermentation time, initial inoculation concentration, medium nutrition
Gram-negative pathogenic bacteria	*E. coli*, *S. enterica*, *Pseudomonas aeruginosa*, *Klebsiella pneumoniae*	marked inhibitory activity against vegetative cells; destroys outer membrane structure of Gram-negative bacteria; inhibits bacterial proliferation	acetic acid, lactic acid, bacteriocins, phenolic metabolites, carbon dioxide	environmental pH, incubation temperature, oxygen concentration, fermentation period
Pathogenic fungi and yeasts	*Aspergillus niger*, *Penicillium*, *Candida albicans*, *Rhizopus stolonifer*	significant antifungal activity; inhibits spore germination and mycelial growth of fungi; suppresses yeast reproduction	phenolic compounds, organic acid mixtures, plantaricin, volatile antibacterial substances	medium sugar content, culture pH, ambient humidity, strain fermentation characteristics
Food spoilage bacteria	common *Spoilage cocci*, *Spoilage bacilli*, *Putrefactive bacteria*	persistent growth inhibition effect; delays bacterial putrefaction metabolism; reduces spoilage metabolite production	composite fermentation metabolites, organic acids, bacteriocin complexes	storage temperature, fermentation maturity, strain activity

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Table 2. Summary of the main antimicrobial substances of *L. plantarum* and their mechanisms of action

Antimicrobial substance	Source/production condition	Key mechanisms of action	Target/effect	Representative data	References
Bacteriocins (e.g., plantaricin)	produced by multiple strains, mainly during logarithmic phase	pore formation, inhibition of cell wall synthesis, suppression of protein synthesis	ion leakage, ATP depletion, ribosome dysfunction, cell membrane damage	20 mm bacteriostatic diameters to *Bacillus species* (JLA-9); 0.1 mg/ml MIC against *Listeria monocytogenes* (NC8)	Zhao et al. (2016); Azzahra et al. (2025); Tobias et al. (2025)
Organic acids (e.g. lactic, acetic, propionic)	produced via glycolysis and mixed-acid fermentation	intracellular pH reduction, penetration of undissociated acid molecules, intracellular anion accumulation	intracellular acidification, enzyme inactivation, osmotic imbalance	10 mmol/l lactic acid reduced *E. coli* viability by 90%	Ribeiro et al. (2021); Liu et al. (2023); Li et al. (2024)
Hydrogen peroxide	synthesised under aerobic conditions, mainly in logarithmic phase	hydroxyl radical generation, thiol oxidation, DNA damage	membrane damage, enzyme inactivation, DNA strand breaks	5 µmol/l H_2O_2 reduced *E. coli* viability by 90%	Bonneville et al. (2021); Chen et al. (2023b); Eben and Imlay (2023)
Lysozyme	accumulated in stationary phase, optimal at pH 6.0	peptidoglycan hydrolysis, membrane disruption, autolysis activation	cell wall thinning, content leakage, cell lysis	10 µg/ml lysozyme reduced *S. aureus* viability by 90%	Venkataramani et al. (2013); Yang and Yan (2025)
Siderophores	induced and secreted under iron-limited conditions	Fe^{3+} chelation, competition for iron, intracellular ROS generation	chelation of Fe^{3+}; competitive iron uptake inhibition; ROS generation after internalisation	production up to 10 µmol/l; reduces free iron to <1 µmol/l	Saha et al. (2016); Page (2019); Lin et al. (2025b)
Short-chain fatty acids (SCFAs)	produced under anaerobic conditions, mainly in stationary phase	GPCR activation (GPR41/43), HDAC inhibition, pH reduction	immunomodulation, altered gene expression, growth inhibition	5 mmol/l propionate reduced *E. coli* viability by 90%	Chang et al. (2024); Raval and Archana (2024)
Exopolysaccharides (EPS)	secreted by multiple strains	physical barrier formation, metal ion chelation, immunomodulation	pathogen adhesion inhibition, iron sequestration, IFN-γ/IL-10 modulation	1 mg/ml EPS inhibited *S. aureus* adhesion	Liu et al. (2017); Silva et al. (2019)
Volatile organic compounds (VOCs)	generated during microbial fermentation	membrane structure damage, enzyme activity inhibition, immunomodulation	increased membrane permeability, reduced metabolic rate	10 µmol/l acetaldehyde reduced *S. aureus* viability by 80%	Zhao et al. (2022); Schastnaya et al. (2023); Chai et al. (2025); Lin et al. (2025a)

Antimicrobial mechanisms of bacteriocins from *L. plantarum*

The antimicrobial activity of bacteriocins produced by *L. plantarum* is mediated through multiple mechanisms. These include the formation of membrane pores leading to the leakage of essential intracellular components, inhibition of the cell wall biosynthesis resulting in bacterial lysis, and disruption of protein synthesis causing growth

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Table 3. Summary of synergistic effects of antimicrobial substances produced by *L. plantarum*

Combination type	Synergistic effect	Optimal concentration/ratio	Brief mechanism	References
Lactic acid + bacteriocin	reduction in *Salmonella* viability	10 : 1 (lactic acid: bacteriocin)	lactic acid increases membrane permeability, facilitating bacteriocin entry into target cells	Lee (2020); Soltani et al. 2022)
Hydrogen peroxide + lysozyme	reduction in *S. aureus* viability	not specified	complementary effects of oxidative damage and cell wall hydrolysis	Xu et al. (2024)
Propionic acid + exopolysaccharides	reduction in *E. coli* viability	not specified	iron sequestration, acidification, and immune activation	Wang et al. (2023)
Hydrogen peroxide + lactic acid	reduction in *Listeria monocytogenes* viability	not specified	synergistic effects of oxidation and acidification	Zhang et al. (2019)
Butyric acid + bacteriocin	reduction in *L. monocytogenes* viability	not specified	HDAC inhibition and membrane-targeting effects	Lee (2020)
Biofilm + lysozyme	reduction in *S. aureus* viability	not specified	synergy between locally high concentrations and exogenous enzyme action	Zhang et al. (2025a)

arrest (Gagandeep et al. 2024). For instance, plantaricin EF exerts its bactericidal effect by binding to specific receptors on the membrane of target pathogens, thereby forming pores approximately 2 nm in diameter. This pore formation induces the efflux of potassium ions and subsequent depletion of intracellular ATP (Zhao et al. 2025). In a separate mechanism, plantaricin GZ1-27 interferes with the bacterial cell wall synthesis by inhibiting key enzymes involved in peptidoglycan assembly, ultimately leading to structural defects and cell death (Du et al. 2022). Additionally, plantaricin lipoprotein lipase-1 (LPL-1) has been shown to impair the ribosomal function, thereby blocking protein synthesis and arresting bacterial growth (Gu et al. 2024).

The mechanistic diversity of these bacteriocins is closely associated with their structural characteristics. Many plantaricin peptides contain conserved motifs such as YGNGV, which facilitate target recognition and receptor binding on bacterial membranes (Ekblad et al. 2016). Beyond their direct antimicrobial effects, bacteriocins derived from *L. plantarum* may also exhibit immunomodulatory properties, potentially stimulate host antibody production and enhance systemic pathogen clearance (Tobias et al. 2025). Experimental evidence further supports the functional potency and stability of these bacteriocins. For example, plantaricin JLA-9, produced by *L. plantarum* JLA-9, generates inhibition zones of up to 20 mm against *Bacillus* species and retains approximately 80% of its activity even after heat treatment at 121 °C for 20 min (Zhao et al. 2016). Similarly, plantaricin NC8 from *L. plantarum* NC8 demonstrates the MIC of 0.1 mg/ml against *Listeria monocytogenes* (Azzahra et al. 2025). These findings underscore the potential of *L. plantarum* bacteriocins as stable and effective antimicrobial agents.

Antimicrobial mechanisms of organic acids from *L. plantarum*

The organic acids produced by *L. plantarum* primarily include lactic acid, acetic acid, and propionic acid, among which lactic acid constitutes the dominant metabolite, accounting for approximately 70% to 90% of the total organic acid yield (Bangar et al. 2022). The capacity of *L. plantarum* to generate organic acids is closely linked to its genomic repertoire of metabolic pathways. Specifically, the presence of a complete glycolytic pathway enables the conversion of glucose to pyruvate and subsequently to lactate (Jang et al. 2023). In addition, under anaerobic conditions, *L. plantarum* is capable of mixed acid fermentation, leading to the production of acetic acid and other organic acids, for

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instance, acetate yields can reach up to 10 mmol/l under oxygen-limited environments (Li et al. 2024). The production of organic acids is also influenced by growth conditions. For example, at an environmental pH of 6.0, *L. plantarum* has been reported to produce lactate at concentrations as high as 20 mmol/l (Liu et al. 2023).

The antimicrobial effects of these organic acids are exerted through several complementary mechanisms. First, they reduce the environmental pH, thereby inhibiting the enzymatic activity of acid-sensitive pathogens. Second, the undissociated forms of organic acids passively diffuse across the bacterial cell membrane and dissociate intracellularly, leading to cytoplasmic acidification. Third, the anionic components of organic acids can bind to intracellular cations, disrupting osmotic balance and causing cellular dysfunction (Rocchetti et al. 2021a). For instance, more than 90% of lactic acid exists in its undissociated form at pH values below 4.0. This lipophilic form penetrates the cell membrane of *E. coli*, reducing intracellular pH to below 5.0 and inhibiting critical enzymatic functions (Hetenyi et al. 2011). Acetic acid, on the other hand, may complex with intracellular potassium ions, inducing osmotic imbalance and resulting in the leakage of cellular contents (Ribeiro et al. 2021). The antimicrobial efficacy of these organic acids is concentration dependent. Lactic acid at a concentration of 10 mmol/l has been shown to reduce the viability of *E. coli* by 90% (El-Garhi et al. 2026). Furthermore, organic acids exhibit synergistic effects when combined with other antimicrobial metabolites. For example, the combination of lactic acid and hydrogen peroxide reduces the survival rate of *Salmonella* by up to 99% (Unal Turhan et al. 2022). The detailed mechanisms of such synergistic interactions are discussed in the following sections.

Antimicrobial mechanisms of hydrogen peroxide from *L. plantarum*

L. plantarum is capable of producing hydrogen peroxide, a function closely associated with the presence of catalase genes within its genome (Wang et al. 2021). For instance, *L. plantarum* ZLP001 harbours a complete catalase gene and has been shown to generate hydrogen peroxide at concentrations reaching 5 µmol/l (Wang et al. 2021). The yield of hydrogen peroxide is strongly influenced by environmental conditions; under aerobic cultivation, production levels can reach up to 10 µmol/l, whereas under anaerobic conditions, they diminish to approximately 1 µmol/l (Bonneville et al. 2021). Furthermore, hydrogen peroxide production is regulated through the modulation of catalase expression. During the logarithmic growth phase, catalase expression has been observed to increase twofold, thereby enhancing the bacterial capacity to produce hydrogen peroxide (Chen et al. 2023b).

The antimicrobial activity of hydrogen peroxide derived from *L. plantarum* operates through several distinct mechanisms. First, it generates hydroxyl radicals that inflict damage upon the cell membranes of pathogenic bacteria. Second, it oxidises thiol groups in bacterial proteins, leading to enzyme inactivation and loss of function. Third, it induces oxidative modification of DNA bases, resulting in strand breaks and genetic damage (Chen et al. 2023b). In *E. coli*, hydrogen peroxide oxidises thiol groups in bacterial proteins, reducing enzymatic activity by 80% (Eben and Imlay 2023). Similarly, exposure to hydrogen peroxide induces oxidative damage to guanine bases in the DNA of *Salmonella*, culminating in DNA fragmentation (Cadet et al. 2008). The antimicrobial potency of hydrogen peroxide is concentration dependent. Moreover, hydrogen peroxide exhibits synergistic effects when combined with other antimicrobial metabolites. The combination of hydrogen peroxide and lactic acid, for instance, has been demonstrated to reduce the survival rate of *Listeria monocytogenes* by up to 99% (Zhang et al. 2019).

Antimicrobial mechanisms of lysozyme from *L. plantarum*

Some strains of *L. plantarum* have been reported to produce lysozyme, but this property is strain-specific while it is not a general characteristic of the species. For instance, *L. plantarum* VSG3 harbours a complete lysozyme gene and it has been shown to produce lysozyme at concentrations reaching 10 µg/ml (Giri et al. 2024). The yield of lysozyme is significantly influenced by environmental conditions. At pH 6.0, lysozyme production by *L. plantarum* can reach up to 15 µg/ml (Venkataramani et al. 2013). Furthermore, the production of lysozyme is regulated through the modulation of gene expression. During the stationary

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growth phase, the expression level of lysozyme has been observed to increase threefold, thereby enhancing the bacterial capacity to produce this antimicrobial enzyme (Liu et al. 2020). It should be noted, however, that not all *L. plantarum* isolates possess lysozyme-encoding genes, and the observed phenotypes cannot be generalised to the entire species without further strain-level evidence.

The antimicrobial activity of lysozyme derived from *L. plantarum* is mediated through several distinct mechanisms. First, it hydrolyses the peptidoglycan layer of the bacterial cell wall, leading to structural defects and compromised integrity. Second, it disrupts the integrity of the cell membrane, resulting in the leakage of intracellular contents. Third, it activates the autolytic system of target bacteria, ultimately inducing the cell lysis (Yang and Yan 2025). Experimental evidence substantiates these mechanisms. For example, lysozyme hydrolyses the peptidoglycan in the cell wall of *S. aureus*, reducing the cell wall thickness from approximately 20 nm to 5 nm (Tanaka et al. 2021). In *E. coli*, lysozyme disrupts the cell membrane integrity, leading to a 90% increase in membrane permeability (Chen et al. 2023a). Moreover, lysozyme activates the autolytic system in *Listeria monocytogenes*, achieving a cell lysis rate of up to 80% (Pasechnek et al. 2020). The antimicrobial efficacy of lysozyme is concentration dependent. At a concentration of 10 μg/ml, lysozyme reduces the viability of *S. aureus* by 90% (Yang and Yan 2025). In addition, lysozyme exhibits synergistic effects when combined with other antimicrobial metabolites. The combination of lysozyme and bacteriocins has been demonstrated to reduce the survival rate of *E. coli* by up to 99% (Ye et al. 2025).

Antimicrobial mechanisms of siderophores from *L. plantarum*

L. plantarum is capable of producing siderophores, a function that is closely associated with the presence of siderophore biosynthesis genes within its genome, indicating that this trait is specific to the strain rather than being a general characteristic of the species. For instance, *L. plantarum* CIDCA 83114 harbours a complete siderophore biosynthesis gene cluster and has been shown to produce siderophores at concentrations reaching 5 μmol/l (Schalk 2025). The yield of siderophores is significantly influenced by environmental iron availability. Under iron-limited conditions, siderophore production by *L. plantarum* can reach up to 10 μmol/l, whereas under iron-replete conditions, production diminishes to approximately 1 μmol/l (Saha et al. 2016; Lin et al. 2025b). Furthermore, the production of siderophores is regulated through the modulation of biosynthetic gene expression. Under iron-deficient conditions, the expression level of siderophore synthesis genes has been observed to increase fivefold, thereby enhancing the bacterial capacity to produce these iron-chelating molecules (Song et al. 2024). Transcriptomic analyses have further revealed that *L. plantarum* can upregulate siderophore-mediated pathways in response to metal stress, enhancing its tolerance to environmental challenges such as selenite exposure (Zhong et al. 2024).

The antimicrobial activity of siderophores derived from *L. plantarum* is mediated through several distinct mechanisms, among which oxidative damage is a key component. First, they chelate ferric iron in the extracellular environment, thereby depriving pathogenic bacteria of this essential micronutrient. Second, they compete with pathogens for iron acquisition, effectively inhibiting their growth. Third, upon internalisation of the siderophore-iron complex by target bacterial cells, the release of iron can generate toxic hydroxyl radicals via Fenton chemistry, leading to cellular damage (Xie et al. 2024). These roles of siderophores with iron limitation coupled with targeted oxidative stress represent a sophisticated antimicrobial strategy, analogous to the iron acquisition and regulation systems controlled by the Fur (ferric uptake regulation) protein in many bacteria. Experimental evidence substantiates these mechanisms. For example, siderophores chelate environmental iron, reducing the available iron concentration to below 1 μmol/l and thereby inhibiting the growth of *E. coli* (Lin et al. 2025b). In competitive assays, siderophores produced by *L. plantarum* reduce iron uptake by *Salmonella* by up to 80% (Khasheii et al. 2021). Furthermore, following the internalisation of the siderophore-iron complex into *Listeria monocytogenes*, the release of intracellular iron promotes hydroxyl radical formation, resulting in oxidative cellular damage (Khasheii et al. 2021). The antimicrobial efficacy of siderophores is closely related to their structural characteristics. Many contain

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conserved catecholate groups that form stable complexes with ferric iron, enhancing their iron-chelating capacity (Rodriguez and Gonzalez-Bello 2023). In addition, siderophores exhibit synergistic effects when combined with other antimicrobial metabolites. The combination of siderophores and organic acids has been demonstrated to reduce the survival rate of *S. aureus* by up to 99% (Page 2019). This synergistic activity may be attributed to the combined effects of iron deprivation and cytoplasmic acidification, which collectively impair pathogen metabolism and viability. Notably, the capacity of probiotics to produce siderophores alongside other antimicrobial compounds such as bacteriocins, lysozymes, and hydrogen peroxides has been recognised as a key mechanism for inhibiting pathogenic bacteria in various applications, including aquaculture (El-Saadony et al. 2021). However, it should be emphasised that the presence and magnitude of siderophore production, as well as the consequent oxidative damage potential, vary considerably among *L. plantarum* isolates, and findings from specific strains should not be generalised for the species as a whole without further evidence.

Antimicrobial mechanisms of SCFAs from *L. plantarum*

L. plantarum is capable of producing SCFAs, including acetate, propionate, and butyrate, a function that is closely associated with the presence of SCFA biosynthesis genes within its genome (Raval and Archana 2024). The capacity for SCFA production varies among strains and is influenced by environmental conditions. For instance, *L. plantarum* Dad-13 has been shown to produce propionate at concentrations reaching 5 mmol/l (Nami et al. 2025), while *L. plantarum* 69-2 generates butyrate at yields of up to 3 mmol/l (Wang et al. 2022a). The production of SCFAs is also significantly influenced by growth conditions. Under anaerobic conditions, SCFA production by *L. plantarum* can reach up to 10 mmol/l, whereas under aerobic conditions, yields diminish to approximately 2 mmol/l (Tomas-Pejo et al. 2023). Furthermore, SCFA production is regulated through the modulation of biosynthetic gene expression. During the stationary growth phase, the expression level of SCFA synthesis genes has been observed to increase threefold, thereby enhancing the bacterial capacity to produce these metabolites (Zhao et al. 2019).

The antimicrobial activity of SCFAs derived from *L. plantarum* is mediated through several distinct mechanisms. First, they activate G protein-coupled receptors (GPCRs) on host cells, including GPR41 and GPR43, thereby modulating immune responses and enhancing pathogen clearance (Ibrahim et al. 2025; Li et al. 2025b). Second, they inhibit histone deacetylase (HDAC) activity in pathogenic bacteria, leading to altered gene expression and growth suppression (Li et al. 2025b). Third, they reduce environmental pH, thereby inhibiting the proliferation of acid-sensitive pathogens (Mukhopadhya and Louis 2025). Experimental evidence substantiates these mechanisms. For example, propionate activates GPR43 on host macrophages, stimulating the production of anti-inflammatory cytokine IL-10 and thereby suppressing inflammatory responses (Li et al. 2025b). Butyrate has been shown to inhibit HDAC-like activity in *E. coli* (specifically, Zn^{2+}-dependent and NAD^{+}-dependent deacetylases such as AcuC and CobB), resulting in an 80% reduction in the expression of virulence-associated genes. Mechanistically, butyrate competes with the natural substrate of these deacetylases, leading to the hyperacetylation of transcription factors that control virulence gene expression (Deng et al. 2025). Acetate reduces environmental pH to below 4.0, thereby inhibiting the growth of *Salmonella species* (Pinhal et al. 2019). Studies have demonstrated that SCFAs produced by *L. plantarum* strains can activate the GPR43-HDAC3 signalling axis, restoring the intestinal barrier integrity and reducing an inflammation (Gao et al. 2022). Furthermore, SCFAs have been shown to modulate the gut microbiota composition, promoting the abundance of beneficial bacteria while suppressing potential pathogens (Mobasherpour et al. 2024; Mukhopadhya and Louis 2025).

The antimicrobial efficacy of SCFAs is concentration dependent. At a propionate concentration of 5 mmol/l, the viability of *E. coli* is reduced by 90% (Chang et al. 2024). In addition, SCFAs exhibit synergistic effects when combined with other antimicrobial metabolites. The combination of butyrate and bacteriocins has been demonstrated to reduce the survival rate of *Listeria monocytogenes* by up to 99% (Lee 2020). This synergistic activity may be attributed to the combined effects of HDAC inhibition, cytoplasmic acidification,

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and membrane disruption, which collectively impair pathogen metabolism and viability. Notably, while SCFAs are well-established HDAC inhibitors in eukaryotic cells, their direct HDAC-inhibitory activity in bacterial systems is less characterised and may be species- or strain-dependent.

Antimicrobial mechanisms of EPS from *L. plantarum*

L. plantarum is capable of producing EPS, which contribute to antimicrobial activity through several distinct mechanisms. First, EPS can form a physical barrier on host cell surfaces, thereby preventing the adhesion and subsequent colonisation of pathogenic bacteria. Second, these biopolymers possess metal-chelating properties, enabling them to sequester essential metal ions from the environment and consequently suppress the pathogen growth. Third, EPS exert immunomodulatory effects by interacting with the host immune cells, thereby enhancing the host capacity to eliminate invading pathogens (Silva et al. 2019; Zhang et al. 2023).

Experimental evidence supports these multifaceted mechanisms. EPS derived from *L. plantarum* ZDY2013 have been shown to form a protective physical barrier that inhibits the adhesion of *Escherichia coli* to Caco-2 intestinal epithelial cells, achieving an inhibition rate of 70% (Zhang et al. 2016). In a separate study, EPS produced by *L. plantarum* WLPL04 demonstrated the capacity to chelate environmental ferric ions, reducing the available iron concentration to below 1 μmol/l and thereby suppressing the growth of *Salmonella* species (Liu et al. 2017). Furthermore, EPS isolated from *L. plantarum* NC8 stimulated the host production of interferon-gamma (IFN-γ), an immunoregulatory cytokine that enhances the clearance of *Listeria monocytogenes* (Niu et al. 2021). The immunomodulatory activity of EPS has also been demonstrated in studies where EPS administration reduced the production of pro-inflammatory cytokines (including TNF-α, IL-1β, and IL-6) while enhancing anti-inflammatory cytokine IL-10, thereby ameliorating inflammatory bowel disease symptoms in murine models (Shukla and Tangney 2025). Additionally, research has confirmed that EPS produced by *L. plantarum* strains can adsorb heavy metals through functional groups such as O-H, C-H, and N-H, which may contribute to their antimicrobial effects through metal ion sequestration (Brdaric et al. 2021).

The antimicrobial efficacy of EPS is closely related to their structural characteristics. The abundance of hydroxyl groups within EPS molecules enables the formation of stable complexes with metal ions, thereby facilitating iron chelation and subsequent pathogen growth inhibition.

Antimicrobial mechanisms of VOCs from *L. plantarum*

L. plantarum produces a variety of VOCs, including acetaldehyde, acetone, ethanol, and other metabolites generated during fermentation (Chai et al. 2025). These VOCs exert antimicrobial effects through several complementary mechanisms. First, they compromise the integrity of pathogenic bacterial cell membranes, leading to the leakage of intracellular contents. Second, they inhibit key enzymatic activities within pathogen cells, resulting in metabolic disruption. Third, certain VOCs modulate host immune responses, thereby enhancing the host ability to eliminate pathogenic microorganisms (Zhao et al. 2022).

The antimicrobial activity of these VOCs has been substantiated through experimental investigations. Acetaldehyde produced by *L. plantarum* has been shown to damage the cell membrane of *S. aureus*, increasing the membrane permeability by 90% (Rocchetti et al. 2021b). Acetone inhibits enzymatic activity in *E. coli*, resulting in an 80% reduction in metabolic rate (Schastnaya et al. 2023). Ethanol derived from *L. plantarum* fermentation stimulates the host production of IL-6, thereby enhancing the clearance of *Salmonella* species (Lin et al. 2025a). Comprehensive metabolomic analyses have revealed that *L. plantarum* fermentation generates a diverse array of volatile compounds, including acids, aldehydes, ketones, and alcohols, which collectively contribute to its antimicrobial properties (Shi et al. 2023).

The antimicrobial efficacy of VOCs is concentration dependent. At an acetaldehyde concentration of 10 μmol/l, the viability of *S. aureus* is reduced by 90% (Rani et al. 2023). Furthermore, VOCs exhibit synergistic effects when combined with other antimicrobial metabolites. The combination of acetaldehyde and lactic acid has been demonstrated to reduce the survival rate of *Listeria*

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monocytogenes by up to 99% (Grahovac et al. 2023). This synergistic activity may be attributed to the combined effects of membrane disruption, enzyme inhibition, and environmental acidification, which collectively impair pathogen viability and metabolic function.

Antimicrobial mechanisms of biofilms from *L. plantarum*

L. plantarum possesses the capacity to form biofilms, a process that proceeds through three distinct stages. The initial stage involves reversible and subsequent irreversible attachment, during which bacterial cells adhere to surfaces through structural components such as flagella and pili. The second stage encompasses aggregation and growth, characterised by the secretion of extracellular polymeric substances including EPS and proteins, leading to the formation of microcolonies. The final stage involves biofilm maturation and dispersion, wherein a structured biofilm community develops and cells are subsequently released to colonise new surfaces (Martinez et al. 2020; Gomez-Mejia et al. 2024). This developmental process exhibits time-dependent characteristics, with significant transcriptional differences observed between attached and dispersed phases (Martinez et al. 2020).

Experimental evidence illustrates these stages across different strains. *L. plantarum* CMPG5300 achieves an adhesion rate of 80% to vaginal epithelial cells through mannose-specific lectins present on its surface (Echegaray et al. 2023). *L. plantarum* WLPL04 secretes EPS that facilitate the formation of microcolonies reaching approximately 10 μm in diameter (Jiang et al. 2016). *L. plantarum* NC8 forms mature biofilms with thicknesses up to 20 μm (Jiang et al. 2018). *L. plantarum* Y42 has been shown to form dense biofilm layers of approximately 18 μm, with biofilm cells exhibiting enhanced autoaggregation ability, hydrophobicity, and adhesiveness compared to their planktonic counterparts (Li et al. 2023a). The ability to form biofilms is influenced by environmental conditions, with biofilm formation rates reaching up to 90% at pH 6.0 (Li et al. 2023a). Strain-specific responses to factors such as fluid flow, nutrient availability, and temperature further modulate the biofilm development (Martinez et al. 2020; Li et al. 2023a; Bui et al. 2025).

The antimicrobial mechanisms exerted by *L. plantarum* biofilms are multifactorial. First, biofilms create a physical barrier that impedes the pathogen adhesion to host surfaces. Second, biofilm-embedded cells continuously secrete antimicrobial substances, creating a locally concentrated inhibitory environment. Third, biofilms modulate host immune responses, thereby enhancing systemic pathogen clearance (Shaaban et al. 2025). Experimental studies substantiate these mechanisms. Biofilms formed by *L. plantarum* CMPG5300 establish a physical barrier that inhibits *E. coli* adhesion to vaginal epithelial cells, achieving inhibition rates of 70% (Malik et al. 2016). *L. plantarum* RX8 biofilms secrete bacteriocins that suppress *Listeria monocytogenes* growth, with inhibition rates reaching 90% (Shen et al. 2025). *L. plantarum* WLPL04 biofilms stimulate the host production of *IL-10*, thereby enhancing the clearance of *Salmonella* species (Jiang et al. 2016. Furthermore, biofilm-formed *L. plantarum* Y42 has demonstrated superior efficacy in inhibiting the adhesion and invasion of *L. monocytogenes* to HT-29 intestinal epithelial cell monolayers compared to planktonic cells, and exhibits enhanced ability to relieve inflammatory reactions and injuries caused by the pathogen infection (Li et al. 2023a). Studies have also demonstrated that postbiotics derived from *L. plantarum* can inhibit the biofilm formation by pathogens such as *L. monocytogenes*, reducing the biofilm formation by 18.70% to 72.48% depending on the concentration (Martinez et al. 2020; Hosseinzadeh et al. 2026).

The antimicrobial efficacy of biofilms is closely related to their structural characteristics. The abundant extracellular polysaccharides within the biofilm matrix form a dense physical barrier that restricts pathogen access to host surfaces (Salas-Jara et al. 2016). Additionally, the three-dimensional architecture of mature biofilms creates microenvironments that concentrate antimicrobial metabolites and facilitate sustained release (Salas-Jara et al. 2016). Biofilms exhibit synergistic effects when combined with other antimicrobial agents. For instance, the combination of *L. plantarum* biofilms with lysozyme reduces *S. aureus* viability by up to 99% (Zhang et al. 2025a). This enhanced efficacy may be attributed to the concentrated local production of antimicrobial compounds within the biofilm matrix, which complements the action of exogenous antimicrobial agents.

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Synergistic antimicrobial effects of multiple components from *L. plantarum*

The antimicrobial efficacy of *L. plantarum* is not attributable to a single metabolite but it rather results from the combined and often synergistic interactions within its diverse arsenal of antimicrobial compounds. These synergistic effects can be broadly categorised into several types: the combination of organic acids with bacteriocins, the concurrent action of hydrogen peroxide and lysozyme, and the interaction between SCFAs and EPS (Soltani et al. 2022). Such combinatorial strategies are increasingly recognised as a key advantage of probiotic-based approaches, as they enhance the antimicrobial potency while potentially mitigating the development of microbial resistance.

Experimental evidence robustly supports the existence of these synergistic interactions. The concurrent application of hydrogen peroxide and lysozyme achieves a 99% reduction in the viability of *S. aureus* (Xu et al. 2024). Furthermore, the combination of propionic acid and EPS has been shown to reduce *E. coli* survival by 99% (Wang et al. 2023). The magnitude of these synergistic effects is highly dependent on the concentration ratios of the combined components. For instance, the synergistic activity between lactic acid and plantaricin is most pronounced when the concentration ratio of lactic acid to bacteriocin is maintained at 10 : 1 (Wang et al. 2022b).

The mechanisms underlying these synergistic antimicrobial effects are multifactorial and operate through complementary pathways. First, certain antimicrobial compounds enhance the membrane permeability of target pathogens, facilitating the intracellular access of other co-administered agents. Second, the combination therapy can inhibit pathogen resistance mechanisms, such as efflux pumps, thereby restoring the susceptibility of resistant strains. Third, these combined metabolites may activate host immune responses, contributing to enhanced systemic pathogen clearance (Roque-Borda et al. 2026).

Specific examples illustrate these mechanistic principles. Lactic acid disrupts the outer membrane of Gram-negative bacteria, thereby enhancing the penetration of bacteriocins such as plantaricin; this synergistic interaction has been shown to reduce the MIC of bacteriocins by 50% (Alakomi et al. 2000; Cheriet et al. 2023). Hydrogen peroxide inhibits the activity of efflux pumps in *E. coli*, effectively reducing the MIC of co-administered bacteriocins by 60% (Alakomi et al. 2000). Propionic acid activates the host GPR43 receptors, stimulating macrophages to produce IL-10 and thereby enhancing the host capacity to eliminate pathogenic bacteria (Lee et al. 2024).

The efficacy of synergistic antimicrobial activity is concentration dependent. When lactic acid reaches a concentration of 10 mmol/l, it reduces the MIC of plantaricin by up to 70% (Lin et al. 2021). Besides enhancing the antimicrobial potency, these synergistic interactions offer the additional advantage of reducing the required dosage of individual antimicrobial agents. This dose-sparing effect minimises potential adverse effects on the host while maintaining or even improving therapeutic efficacy (Roque-Borda et al. 2026). The capacity of *L. plantarum* to simultaneously produce multiple synergistic antimicrobial metabolites underscores its potential as a source of novel combination therapies for combating multidrug-resistant pathogens.

CHALLENGES AND FUTURE PERSPECTIVES

Safety assessment of *L. plantarum*

Safety assessment constitutes a fundamental prerequisite for the application of *L. plantarum* in food and pharmaceutical sectors. Current research has primarily focused on three critical dimensions: antibiotic resistance profiles, virulence determinants, and metabolic safety (Chokesajjawatee et al. 2020; Zhu et al. 2024).

Regarding the antibiotic resistance, most *L. plantarum* strains remain susceptible to clinically relevant antibiotics, although strain-specific resistance phenotypes have been documented. For instance, *L. plantarum* SKI19 exhibits an erythromycin MIC of 16 μg/ml, exceeding the EFSA-recommended threshold of 8 μg/ml (Botthoulath et al. 2018). More concerning is the potential for horizontal gene transfer; the *tetM* gene harboured by *L. plantarum* MTCC 5690 has been demonstrated transferable to *S. aureus* under laboratory conditions (Wijaya et al. 2025). Genomic analyses have further revealed that some strains carry multidrug resistance transporters potentially mediating resistance

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to both plant secondary metabolites and antibiotics (Mariault et al. 2025).

With respect to virulence factors, comprehensive genomic evaluations indicate that most strains lack pathogenic determinants. Nevertheless, certain strains present safety concerns. *L. plantarum* MF1298 carries the *HDC* gene encoding histidine decarboxylase, which can lead to histamine accumulation in fermented products reaching 50 mg/kg (Engevik et al. 2024). Biogenic amine production has thus been identified as a strain-specific trait requiring careful evaluation.

Regarding the metabolic safety, D-lactic acid produced by *L. plantarum* warrants particular attention due to its potential to induce lactic acidosis in susceptible populations. In patients with renal insufficiency, daily intake of 1×10^{11} CFU has been shown to elevate blood D-lactate levels from 0.5 mmol/l to 2.0 mmol/l (Kim and Jung 2020). The safety profile exhibits pronounced strain specificity: *L. plantarum* 299v is widely recognised as safe with GRAS status, whereas *L. plantarum* MF1298 presents risks associated with biogenic amine production (Huang et al. 2025). Furthermore, safety outcomes are significantly influenced by dosage; daily intakes below 1×10^{10} CFU are typically well-tolerated, while doses exceeding 1×10^{11} CFU may trigger gastrointestinal discomfort (Moses 2021). These findings provide a foundational framework for safety assessment, yet the establishment of unified international evaluation standards remains an imperative priority.

Individual variability in responsiveness to *L. plantarum*

Individual variability in the antimicrobial efficacy of *L. plantarum* represents a significant challenge for its widespread application. This heterogeneity is primarily attributable to host-specific factors, including gut microbiota composition, genetic background, and lifestyle characteristics (Jiang et al. 2025a). Regarding the gut microbiota, the ratio of *Bacteroidetes* to *Firmicutes* (B/F ratio) has been shown to influence the colonisation capacity of *L. plantarum*. In hosts with a high B/F ratio, colonisation rates reach approximately 80%, whereas in those with a low ratio, colonisation is reduced to only 40% (Tsai et al. 2025). Recent evidence further demonstrates that the gut microbiota can drive structural variations in exogenous *L. plantarum* strains, enhancing their colonisation ability through adaptive evolution under intestinal selective pressure (Jiang et al. 2025b).

The host genotype constitutes another critical determinant of responsiveness. Polymorphisms in the host *TLR2* gene, for instance, modulate the immunomodulatory effects of *L. plantarum*. Individuals carrying the CC genotype at the TLR2 rs5743708 locus exhibit a twofold increase in IFN-γ secretion following *L. plantarum* administration, whereas those with the TT genotype show no significant immune response (Terasjarvi et al. 2024). This genotype-dependent variation underscores the importance of the host genetic background in mediating probiotic-host interactions.

Lifestyle factors further contribute to response variability. Smoking has been associated with the reduced antimicrobial activity of *L. plantarum*, when the intestinal abundance of *L. plantarum* in smokers is approximately $1 \times \log_{10}$ CFU/g lower than in non-smokers, accompanied by a 30% reduction in the pathogen inhibition capacity (Shapiro et al. 2022). Notably, individual differences in response exhibit pronounced strain specificity. *L. plantarum* P8 demonstrates more significant anxiety-relieving effects in women, while *L. plantarum* 299v shows greater efficacy in men (Lew et al. 2019). Furthermore, age significantly influences responsiveness; response rates reach 80% in young adults but they decline to 50% in the elderly population (Yang et al. 2024; Aljohani et al. 2025). These findings provide a foundation for personalised probiotic applications, yet the development of predictive models incorporating multi-dimensional host factors remains an imperative research priority.

Standardisation challenges in *L. plantarum* research

Standardisation represents a critical challenge limiting the advancement of *L. plantarum* research, primarily manifesting as inconsistencies in strain identification, experimental methodologies, and evaluation criteria. Regarding the strain identification, the widely employed 16S rRNA gene sequencing method exhibits insufficient discriminatory power to differentiate closely related taxa; the 16S rRNA gene sequences of *L. plantarum* and *L. pentosus* share up to 99.9% similarity (Skotniczny and Satora 2023). Alternative molecular markers

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such as pheS or recA have been proposed for improved resolution, yet no universal consensus has been established (Pot et al. 2019). Furthermore, discrepancies in the strain nomenclature persist across different laboratories; for instance, *L. plantarum* 299v is alternatively designated as DSM 9843 (Chatsirisakul et al. 2025).

With respect to experimental methodologies, conditions for *in vitro* antibacterial assays remain inadequately harmonised. Some investigations employ agar diffusion methods, whereas others utilise broth microdilution techniques, yielding results that are not directly comparable (Hossain 2024). Evaluation criteria for antibacterial activity, including inhibition zone diameters, MIC values, and minimum bactericidal concentration (MBC) values, lack universally accepted reference standards (Kaderabkova et al. 2024). These methodological inconsistencies are particularly pronounced in clinical trials, where variations in dosage regimens, administration routes, and outcome assessment criteria impede meaningful meta-analysis and evidence synthesis (Hacke and Nunan 2020; Pfaffenlehner et al. 2025). Moreover, standardisation varies considerably across disciplinary domains; the food sector demonstrates a relatively higher degree of methodological uniformity, whereas the clinical medicine sector exhibits greater heterogeneity (van de Kaa 2023). These findings underscore the necessity for establishing harmonised, cross-disciplinary standards to facilitate robust comparative analyses and accelerate translational applications.

Consistency of antimicrobial activity in *L. plantarum* research

The consistency of antimicrobial activity represents a significant challenge for the application of *L. plantarum*, with efficacy being influenced by strain-specific characteristics, cultivation parameters, and application matrices. Substantial inter-strain variability in antimicrobial potency has been documented. For instance, *L. plantarum* DY-6 exhibits 90% inhibition against *E. coli*, whereas *L. plantarum* ATCC 8014 achieves only 50% inhibition under comparable conditions (Baillo et al. 2022).

Culture conditions exert profound effects on antimicrobial consistency. Optimal bacteriocin production is typically achieved following 24 h of incubation at 37 °C and pH 5.5, whereas production diminishes by approximately 50% under suboptimal conditions of 30 °C and pH 7.0 (Elazzazy et al. 2024). Application scenarios further modulate antimicrobial efficacy; in protein-rich food matrices, *L. plantarum* maintains approximately 90% of its antimicrobial activity, whereas in carbohydrate-rich environments, the activity retention decreases to 70% (Echegaray et al. 2023).

Notably, consistency exhibits pronounced strain specificity: the antimicrobial activity of *L. plantarum* 299v remains stable across experimental replicates, whereas that of *L. plantarum* MF1298 displays a significant fluctuation (Chen et al. 2024). Storage conditions critically influence the long-term stability; after six months of storage at 4 °C, the activity retention reaches 80%, compared to only 40% at 25 °C (Kuzman et al. 2021). These findings provide guidance for optimising consistency, however, the establishment of comprehensive quality control systems incorporating standardised production parameters remains an essential priority for industrial application.

CONCLUSION

L. plantarum demonstrates a considerable potential for applications in food preservation, healthcare, and agricultural biocontrol owing to its broad-spectrum antimicrobial activity and favourable safety profile. Its antimicrobial effects are mediated by diverse metabolites, notably bacteriocins, organic acids, hydrogen peroxide, lysozyme, siderophores, and SCFAs. Biofilm formation and synergistic interactions among these compounds further enhance efficacy, supporting the development of novel antimicrobial agents.

Nevertheless, several challenges constrain its application. Safety assessment requires standardised protocols, particularly concerning transferable resistance genes and metabolic risks. Host-specific factors, including genetic background, age, and gut microbiota composition, contribute to response heterogeneity, necessitating personalised approaches. Standardisation deficits in strain identification, experimental methodologies, and clinical trial design impede cross-study comparability. Additionally, the consistency of antimicrobial efficacy is influenced by strain stability, production processes, and storage conditions, requiring robust quality control systems.

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In summary, *L. plantarum* represents a promising natural antimicrobial agent. Future research should prioritise multi-omics elucidation of strain-specific determinants, establishment of standardised evaluation frameworks, characterisation of host-microbe interactions, and optimisation of fermentation and formulation technologies to facilitate its efficient and safe translation from laboratory research to practical implementation.

Conflict of interest

The authors declare no conflict of interest.

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