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RESEARCH ARTICLE

Quorum-quenching potential of *Limosilactobacillus fermentum* UAS LAB 6 oxidoreductase against dairy spoilage and plant pathogenic *Pseudomonas* sp.: A computational perspective

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Abstract

Quorum-sensing (QS) regulates bacterial communication through N-acyl homoserine lactones (AHLs), which coordinate critical functions such as biofilm formation, virulence and spoilage activity. Disruption of this signaling, termed quorum-quenching (QQ), offers a sustainable strategy to mitigate pathogenicity without promising resistance. In this study, *Limosilactobacillus fermentum* UAS LAB 6, a lactic acid bacterium with known probiotic potential, was investigated for its ability to produce oxidoreductase enzymes capable of AHL modification. Whole-genome sequencing and annotation revealed multiple oxidoreductase candidates, of which a short-chain dehydrogenase/reductase (SDR) was selected for *in silico* characterization. Active site prediction and molecular docking analyses were performed using AutoDock Vina in PyRx 1.2 to evaluate enzyme interactions with AHL molecules produced by *Pseudomonas fluorescens*, *P. syringae* and *P. corrugata*. Docking results demonstrated high binding affinities, particularly between the SDR enzyme and 3-oxo-C14-HSL (ΔG = -7.4 kcal/mol), indicating strong substrate-enzyme interactions. The oxidoreductase exhibited a substrate preference toward long-chain and 3-oxo-substituted AHLs, consistent with its potential role in reducing the C3-oxo group to inactive 3-hydroxy derivatives. These findings suggest that *L. fermentum* oxidoreductases may effectively interfere with AHL-mediated signaling in plant-pathogenic and dairy spoilage *Pseudomonas* spp. Overall, this study highlights the dual quorum-quenching potential of LAB-derived oxidoreductases, offering an eco-friendly strategy to enhance plant health and food safety and through microbial signal disruption.

Keywords: acyl homoserine lactone; *Limosilactobacillus fermentum*; molecular docking; oxidoreductase; *Pseudomonas* sp.; quorum-quenching

Introduction

Microbial communication through quorum-sensing (QS) enables bacteria to regulate gene expression in response to population density, coordinating key physiological processes such as biofilm formation, motility and the production of extracellular enzymes and virulence factors. This cell–cell signaling typically involves N-acyl homoserine lactones (AHLs) in Gram-negative bacteria, which bind to LuxR-type receptors to activate QS-regulated genes once a threshold concentration is reached (1). In food-associated bacteria such as *Pseudomonas fluorescens*, AHL-mediated QS regulates proteolytic and lipolytic enzymes responsible for spoilage, contributing to reduced product quality and shelf life. Similarly, plant-pathogenic *Pseudomonas* species such as *Pseudomonas syringae* and *Pseudomonas corrugata* utilize AHLs to coordinate virulence traits including phytotoxin production, motility and biofilm formation on host tissues, leading to significant agricultural losses (2).

The inhibition or disruption of QS, termed quorum-quenching (QQ), represents a promising and sustainable strategy to mitigate pathogenicity and spoilage without exerting selective pressure for antibiotic resistance (3). Recent research continues to explore novel quorum-quenching enzymes, including thermostable lactonases and redox-active oxidoreductases, for biocontrol and food safety applications (4). QQ enzymes inactivate or modify AHLs through mechanisms such as hydrolysis, acyl chain cleavage, or redox modification. These enzymes include lactonases, acylases and oxidoreductases. The most extensively studied QQ enzymes include lactonases (EC 3.1.1) and acylases (EC 3.5.1), which hydrolyze or cleave AHLs irreversibly (5). However, relatively fewer studies have focused on oxidoreductases (EC 1), which can reversibly modify AHLs by reducing the 3-oxo group to a 3-hydroxy derivative, effectively rendering the signal molecule inactive while maintaining its structural integrity (6).

Such redox-based QQ enzymes are increasingly recognized for their ecological versatility. The metagenomic discovery of the NADP-dependent short-chain dehydrogenase/reductase (SDR) BpiB09 demonstrated its ability to inactivate AHLs and attenuate *Pseudomonas aeruginosa* virulence and biofilm formation (6).

Similarly, other studies have shown that SDR-type oxidoreductases from environmental isolates can reduce AHL-dependent signaling in diverse bacterial species (7). The reversible modification of AHLs by oxidoreductases provides an advantage over hydrolytic degradation, as it minimizes the emergence of resistant strains while maintaining environmental compatibility (8).

Lactic acid bacteria (LAB), including *Limosilactobacillus fermentum*, are well known for their probiotic activity and ability to secrete antimicrobial compounds, bacteriocins and metabolic enzymes. Recent studies have demonstrated that *L. fermentum* exhibits strong antimicrobial and probiotic potential, supported by complete genome analyses revealing diverse oxidoreductase and redox-related enzymes (9, 10). Functional genomics of *L. fermentum* LAB-1 and JNU532 have revealed multiple genes encoding oxidoreductases and dehydrogenases, which may contribute to redox homeostasis and quorum-quenching–like activities through AHL modification. Moreover, lactic acid bacteria have been shown to inhibit QS and biofilm formation in *P. aeruginosa* and related spoilage organisms *via* production of secondary metabolites and enzymes (11).

In parallel, *P. syringae* and *P. corrugata*, which cause diseases such as bacterial speck and tomato pith necrosis respectively, rely on AHL-mediated QS for pathogenesis. *P. corrugata*, for instance, employs the PcoI/PcoR system to synthesize and detect AHLs (mainly 3-oxo-C6-HSL and C6-HSL) that regulate phytotoxin production and biofilm development (12). Disruption of this signaling pathway leads to a marked reduction in virulence. Likewise, *P. syringae* QS controls expression of toxins and extracellular enzymes that facilitate infection and colonization of plant tissues (13).

Given the structural conservation of AHLs across *Pseudomonas* species, it is plausible that oxidoreductases from *L. fermentum* could act broadly against AHLs produced by both food spoilage and plant-pathogenic *Pseudomonas* spp. This dual QQ potential highlights the relevance of LAB-derived enzymes in promoting sustainable food preservation and plant protection strategies.

Therefore, the present study employs *in silico* genome mining, active site prediction and molecular docking to characterize the oxidoreductase-mediated interactions between *L. fermentum* UAS LAB 6 and AHL molecules from *P. fluorescens*, *P. syringae* and *P. corrugata*. The study aims to elucidate the enzyme's substrate specificity and molecular basis for AHL recognition, offering insights into the potential application of LAB-derived oxidoreductases as eco-friendly biocontrol agents in both dairy and agricultural ecosystems.

Materials and Methods

Isolation and genome-based identification of oxidoreductase enzyme

L. fermentum UAS LAB 6 (Accession No. PV687706), previously identified as a quorum-quenching strain, was obtained from the Department of Agricultural Microbiology, GKVK, UAS, Bangalore, Karnataka, India. The strain was maintained on MRS agar at 4 °C and subcultured in MRS broth at 37 °C for 18–24 hr prior to genomic DNA extraction. Genomic DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Germany) following the manufacturer's protocol. Whole genome sequencing was carried out on the Illumina NovaSeq 6000 platform using a paired-end (2 × 150 bp) library with an average sequencing depth of approximately 120×. Raw reads were quality-checked using FastQC (v0.11.9) and trimmed with Trimmomatic (v0.39) to remove adapters and low-quality bases. High-quality filtered reads were assembled using SPAdes v3.15.3 and the draft genome was annotated using the NCBI Prokaryotic Genome Annotation Pipeline (PGAP). Annotation revealed multiple oxidoreductase genes, which were further characterized using BLASTp (NCBI non-redundant protein database, E-value ≤ $1e^{-5}$, identity ≥ 40 %, coverage ≥ 70 %) and RAST server (version 2.0). Candidate enzymes were classified based on predicted cofactor-binding motifs and enzyme families and the oxidoreductase showing the highest sequence homology (≥ 90 % identity and ≥ 80 % query coverage) to known quorum-quenching or redox-active proteins was selected for molecular docking studies. Among the identified oxidoreductases, the short-chain dehydrogenase/reductase (SDR) was prioritized for molecular docking due to its high sequence similarity, conserved catalytic motifs ((Ser-Tyr-Lys) and precedent in the literature showing that NADP-dependent SDR enzymes (e.g., BpiB09) can modify AHL quorum-sensing signals and attenuate virulence and biofilm formation in Gram-negative bacteria (6).

Ligand preparation

Six AHL molecules associated with the quorum-sensing system of these *Pseudomonas* sp. were selected as ligands for docking analysis. Their molecular structures and properties were retrieved from the PubChem database (NCBI) in SDF format. The ligands, representing short-chain, medium-chain and long-chain AHLs, were used to evaluate oxidoreductase-AHL interactions (Table 1).

Table 1. AHL molecules from *Pseudomonas* spp. used as ligands in molecular docking, with PubChem IDs

Sl. No.	AHL molecules produced by *Pseudomonas* sp.	Compound ID	References
1	3-oxo-C6-HSL	688505	(14)
2	C8-HSL	6914579	(14)
3	C6-HSL	10058590	(15)
4	C4-HSL	10130163	(16, 17)
5	C10-HSL	10131281	(15, 16)
6	3-oxo-C14-HSL	9883786	(17)

Active site prediction

To identify the specific regions of the enzyme involved in ligand interaction, the active site residues of the modelled oxidoreductase were predicted using the CASTpFold server (version 3.0) with default parameters, including a probe radius of 1.4 Å and the calculation of pocket and cavity volumes using the Richards' surface algorithm.

Molecular docking

Docking was performed using PyRx version 1.2 integrated with the AutoDock Vina engine (18). The 3D structure of the oxidoreductase enzyme was generated using the SWISS-MODEL server with the crystal structure of short-chain dehydrogenase/reductase (PDB ID: 9FE6) as the modeling template. The selected template showed 88.7 % sequence identity and 96 % sequence coverage with the query enzyme. The resulting model exhibited a GMQE score of 0.81 and a QMEANDisCo global score of 0.75 ± 0.05, indicating high model reliability. Stereochemical validation using PROCHECK revealed that >90.0 % of residues were in favored regions of the Ramachandran plot, confirming good stereochemical quality. These parameters collectively validate the structural integrity of the model for

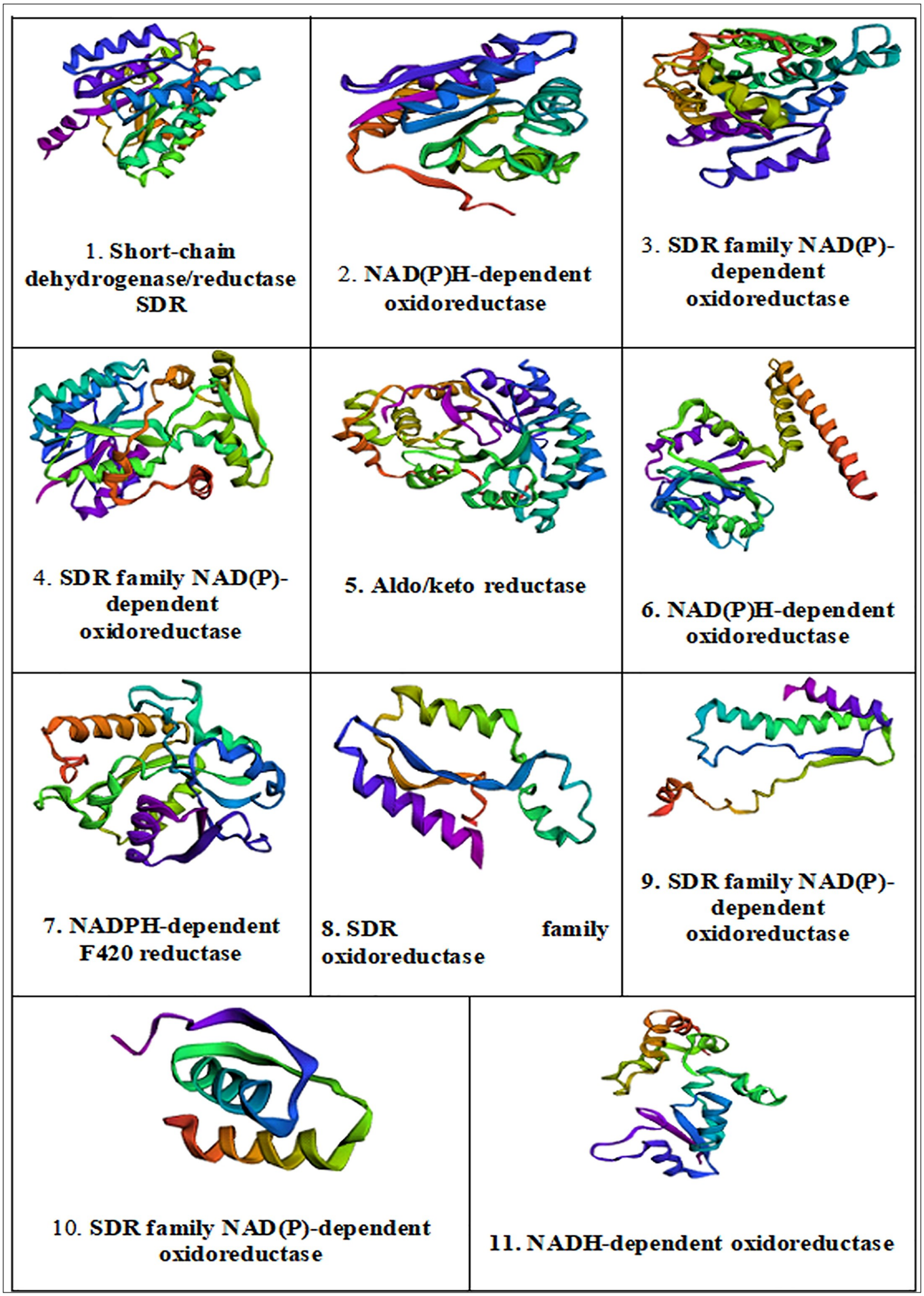

Fig. 1. Predicted 3D structures of oxidoreductase enzymes from *L. fermentum* UAS LAB 6 generated using SWISS-MODEL server (version 4.2) based on homology modeling. Model validation was performed using PROCHECK and Verify3D, confirming acceptable stereochemical quality. Structural domains and active-site regions are shown. These models were used as receptors for AutoDock Vina docking analyses.

downstream docking and interaction analyses. The modelled oxidoreductase, constructed and energy-minimized using SWISS-MODEL, was used as the receptor (Fig. 1) and the selected AHL molecules served as ligands. Prior to docking, the receptor protein was prepared by removing all water molecules, adding polar hydrogens, assigning Kollman charges and performing energy minimization using the Universal Force Field (UFF). Docking grids were centered on the predicted active site coordinates given in supplementary data (Supplementary Table 1) and an exhaustiveness value of 8 was used to ensure accurate conformational sampling. Binding affinities (kcal/mol) and interaction profiles were evaluated for each enzyme-ligand complex to identify key residues involved in ligand recognition and stability, thereby assessing the enzyme's quorum-quenching potential. The corresponding dissociation constants (*Kd*) were estimated from the docking-derived binding free energies using the thermodynamic relation $\Delta G = RT \ln (Kd)$, assuming a temperature of 298 K and standard state conditions. This approach provides an approximate measure of ligand–enzyme affinity consistent with previous computational studies (18). Docked complexes were visualized and analyzed using Discovery Studio Visualizer v21.1.0 and PyMOL v2.5 for interaction mapping and 3D structural interpretation.

Results and Discussion

Molecular docking using AutoDock Vina in PyRx 1.2 was performed to evaluate interactions between the modelled oxidoreductase enzymes of *L. fermentum* UAS LAB 6 and AHL molecules of *P. fluorescens, P. syringae* and *P. corrugata*. Multiple ligand conformations were generated and ranked based on binding affinities (kcal/mol), with the lowest Gibbs free energy values representing the most stable complexes given in supplementary data (Supplementary Table 2). Top-ranked poses were analyzed to infer the enzyme's quorum-quenching potential (Table 2). Docking results provided insights into the molecular mechanisms by which LAB-derived oxidoreductases may interfere with AHL-mediated signaling. Comparable studies have shown that AHLs typically exhibit stable binding to quorum-quenching enzyme active sites, supporting their role in signal disruption (19). Binding energies ranging from -5 to -8 kcal/mol are generally indicative of biologically relevant interactions (20). Additionally, variations in AHL chain length and substituent groups can influence enzyme affinity and catalytic efficiency (21).

Molecular docking analysis revealed varying binding affinities of oxidoreductase enzymes from *L. fermentum* UAS LAB 6 towards the AHL signaling molecules of *Pseudomonas* sp.. Among the eleven oxidoreductases examined, the short-chain dehydrogenase/reductase (SDR) exhibited the strongest interaction, particularly with 3-oxo-C14-HSL (ΔG = -7.4 kcal/mol; $Kd = 3.74 \times 10^{-6}$ M), followed by C8-HSL (ΔG = –6.8 kcal/mol), indicating high affinity toward long-chain AHLs. Other SDR family members and NAD(P)-dependent oxidoreductases also showed favorable binding energies ranging between -6.4 and -6.9 kcal/mol, suggesting their potential role in targeting both medium-chain and long-chain AHLs. Moderate affinities were observed for NAD(P)H-dependent and aldo/keto reductases ($\Delta G \approx$ -5.6 to -6.0 kcal/mol), whereas the NADPH-dependent F420 reductase and certain SDR variants displayed comparatively lower binding energies ($\Delta G \approx$ -5.5 to -5.9 kcal/mol). Notably, weaker interactions were recorded with short-chain AHLs such as C4-HSL (ΔG = -4.8 kcal/mol), reflecting substrate preference toward extended acyl chains and 3-oxo-substituted derivatives. These results align with prior studies that demonstrated the ability of oxidoreductases to inactivate AHLs by reducing the oxo-group at the C-3 position, thereby generating inactive 3-hydroxy derivatives and attenuating QS (22). Comparable trends have been reported in recent quorum-quenching studies where oxidoreductases and lactonases exhibited selective binding toward long-chain and 3-oxo-substituted AHLs (4). The SDR enzyme exhibited highest binding affinity toward long-chain AHLs such as 3-oxo-C14-HSL from *P. fluorescens*, followed by medium-chain analogs (C8-C10-HSL) produced by *P. syringae* and *P. corrugata*. These consistent affinities across species suggest a conserved quorum-quenching potential targeting both spoilage and plant-pathogenic *Pseudomonas* spp. (6). The comparatively lower binding affinities observed for short-chain AHLs such as C4-HSL may be attributed to their reduced hydrophobic interactions and weaker van der Waals contacts within the oxidoreductase binding pocket. These molecules possess

Table 2. AutoDock Vina binding energies (ΔG) and predicted dissociation constants (*Kd*) for oxidoreductases of *L. fermentum* UAS LAB 6 docked with AHL ligands

Sl. No.	Protein	Ligand	Binding energy ΔG (kcal mol^{-1})	Dissociation constant *Kd* (M) at 25 °C
1	Short-chain dehydrogenase/reductase SDR	3-oxo-C14-HSL	–7.4	3.74e-06
		C8 HSL	–6.8	1.03e-05
2	NAD(P)H-dependent oxidoreductase	3-oxo-C14-HSL	–6.0	3.97e-05
		C10-HSL	–5.9	4.71e-05
3	SDR family NAD(P)-dependent	3-oxo-C14-HSL	–6.9	8.69e-06
		3-oxo-C6-HSL	–6.4	2.02e-05
4	SDR family NAD(P)-dependent oxidoreductase	3-oxo-C6-HSL	–6.6	1.44e-05
		C10-HSL	–6.5	1.71e-05
5	Aldo/keto reductase	C8 HSL	–5.9	4.71e-05
		C10-HSL	–5.6	7.81e-05
6	NAD(P)H-dependent oxidoreductase	3-oxo-C14-HSL	–6.6	1.44e-05
		3-oxo-C6-HSL	–6.5	1.71e-05
7	NADPH-dependent F420 reductase	3-oxo-C6-HSL	–5.9	4.71e-05
		C10-HSL	–5.9	4.71e-05
8	SDR family oxidoreductase	C10-HSL	–5.6	7.81e-05
		C8-HSL	–5.5	9.25e-05
9	SDR family NAD(P)-dependent oxidoreductase	C4-HSL	–4.8	3.02e-04
		3-oxo-C14-HSL	–4.8	3.02e-04
10	SDR family NAD(P)-dependent oxidoreductase	C8 HSL	–4.7	3.57e-04
		3-oxo-C14-HSL	–4.7	3.57e-04
11	NADH-dependent oxidoreductase	C10-HSL	–5.7	6.60e-05
		3-oxo-C6-HSL	–5.3	1.30e-04

shorter acyl chains that limit stabilization within the enzyme's hydrophobic cavity, resulting in less favorable docking energies. This finding is consistent with the ecological and pathogenic behaviour of *Pseudomonas* species where, long-chain and 3-oxo-substituted AHLs (e.g., 3-oxo-C10-HSL, 3-oxo-C14-HSL) are the predominant signals regulating biofilm formation, protease production and virulence expression. Short-chain AHLs typically mediate less complex regulatory networks and are more common in non-pathogenic or opportunistic *Pseudomonas* strains (23).

The broad substrate specificity of the SDR enzyme toward medium-chain AHLs (C6–C10) aligns with reports that many quorum -quenching oxidoreductases exhibit greater affinity for long-chain and 3-oxo-substituted AHLs than for short-chain analogs (20). This preference is particularly relevant to many *Pseudomonas* spp., such as *P. fluorescens*, a dairy spoilage organism. Similarly, *P. syringae* and *P. corrugata*, which are plant pathogenic bacteria, rely on long-chain AHL-mediated QS for biofilm formation, virulence and protease secretion. Other oxidoreductases, including NAD(P)H-dependent and aldo/keto reductases, demonstrated moderate affinities across different AHLs. The selective binding of aldo/keto reductase to C8-HSL indicates enzyme-specific substrate targeting, consistent with earlier findings that variations in AHL chain length influence degradation efficiency (24).

Mechanistically, oxidoreductases differ from lactonases and acylases as they modify rather than cleave AHL molecules typically reducing the 3-oxo group to a 3-hydroxy derivative, rendering them inactive to LuxR-type receptors (8).

Moreover, enzymatic quorum-quenching mechanisms provide greater specificity and environmental safety than traditional chemical quorum-sensing inhibitors like halogenated furanones or synthetic analogs. Chemical QS inhibitors typically function by blocking signal perception or synthesis, which may interfere with multiple bacterial pathways or lead to cytotoxicity. In contrast, biological QQ through enzymes such as oxidoreductases and lactonases acts directly on signal molecules, modifying or degrading them without imposing strong selective pressure for resistance. This enzyme-based approach preserves beneficial microbial communities and ensures biocompatibility in food and environmental applications (8).

The docking results suggest that *L. fermentum* oxidoreductases may act as natural QQ agents by interfering with AHL-mediated communication in *P. fluorescens*, *P. syringae* and *P. corrugata*, thereby reducing their biofilm formation, virulence and spoilage potential. These findings highlight the potential of LAB-derived enzymes as eco-friendly alternatives to chemical preservatives for controlling plant diseases and microbial spoilage in dairy environments (25).

Although direct biochemical confirmation of oxidoreductase -mediated AHL degradation by *L. fermentum* or other lactic acid bacteria (LAB) is still limited, emerging evidence suggests that LAB can interact with and influence the quorum-sensing (QS) systems of Gram-negative bacteria. For instance, *Lactiplantibacillus plantarum* WCFS1 has been shown to exhibit transcriptional and proteomic responses to the QS molecule N-(3-oxododecanoyl)-L-homoserine lactone (3-oxo-C12-HSL) from *P. aeruginosa*, indicating its ability to sense and potentially interfere with AHL-mediated communication (26). Moreover, QQ activities have been reported in several non-LAB bacteria inhabiting food and aquatic environments, where enzymes such as lactonases, acylases and oxidoreductases degrade AHLs and attenuate microbial virulence (27). These findings, though indirect, support the ecological relevance of LAB–QS interactions and provide a rationale for the present study's computational exploration of LAB oxidoreductases as potential QQ agents. By demonstrating the possible AHL-modifying ability of LAB-derived enzymes, this study adds to the growing evidence that probiotic microorganisms may play an important role in modulating microbial signaling and maintaining food ecosystem stability.

While molecular docking provides valuable insights into potential enzyme-substrate interactions, it represents a static approximation that does not fully account for the dynamic flexibility of enzyme active sites or solvent-mediated effects that can influence ligand binding and catalysis. These limitations may lead to minor deviations between predicted and experimental binding affinities. Therefore, future studies incorporating molecular dynamics simulations and wet-lab validation are warranted to refine these predictions (28).

These computational analyses demonstrate strong SDR–AHL interactions. However, the stability and activity of the enzyme under practical conditions remains to be established. In real dairy and plant ecosystems, factors such as pH fluctuations, temperature variation and organic load could influence the catalytic turnover and persistence of SDR. Therefore, future experimental validation focusing on enzyme kinetics, environmental stability and formulation feasibility will be crucial to determine its effectiveness and durability in applied settings (29). Such investigations will provide essential insights into translating the observed *in silico* quorum-quenching activity into viable industrial and agricultural applications.

The use of redox-based quorum-quenching enzymes such as oxidoreductases may have broader ecological implications. These enzymes modulate microbial communication without exerting bactericidal pressure, thereby reducing resistance development and maintaining microbial diversity (30). By disrupting signaling rather than killing cells, redox-active QQ enzymes can alter nutrient fluxes and biochemical interactions in complex ecosystems (31). However, understanding how these enzymes influence microbial balance and long-term ecological stability requires further community-level and environmental studies.

From an applied perspective, the QQ potential of *L. fermentum* or its purified oxidoreductase enzymes could be harnessed in the development of bio-based products for industrial use. In the dairy sector, incorporating *L. fermentum*–derived cell-free extracts or enzyme preparations into sanitizing formulations or bio-coating materials may help prevent biofilm development on processing equipment, thereby improving product hygiene and extending shelf life. Likewise, the enzyme's ability to disrupt AHL-mediated signaling in plant-pathogenic *Pseudomonas* spp. supports its potential role in sustainable biocontrol formulations aimed at suppressing bacterial virulence and disease incidence (32). Such applications align with ongoing efforts to replace synthetic antimicrobials with safe, natural and biodegradable alternatives, reinforcing the industrial and ecological significance of LAB-derived QQ systems.

Conclusion

This study provides computational evidence supporting the quorum -quenching potential of oxidoreductase enzymes from *L. fermentum*

UAS LAB 6. The identified SDR displayed high affinity for AHL molecules, particularly long-chain and 3-oxo-substituted derivatives, indicating its likely ability to modify and inactivate quorum-sensing signals. By targeting AHLs from *P. fluorescens* (a dairy spoilage bacterium) and the plant pathogens *P. syringae* and *P. corrugata*, the enzyme demonstrated a broad substrate specificity that can be used for both food preservation and plant disease management. The reversible redox-based modification of AHLs offers a promising, resistance-free alternative to traditional antimicrobial interventions. These findings position LAB-derived oxidoreductases as multifunctional biocontrol agents that can contribute to sustainable microbial management in agricultural and food systems. Future studies may include *in vitro* validation of the predicted quorum-quenching activity of oxidoreductases through enzyme kinetics and AHL degradation assays. Recombinant expression and purification of the SDR enzyme could be followed by spectrophotometric NAD(P)H-coupled activity assays and quantitative assessment of AHL turnover could be performed using high-performance liquid chromatography (HPLC) or mass spectrometry.

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Authors' contributions

HMV conducted the experiments, analyzed the data and prepared the initial draft of the manuscript. HMV and TK conceptualized the experiment. TK reviewed the manuscript for language, supervised the work and provided suggestions to improve data interpretation. Both authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Quill Bot and Chat GPT in order to improve writing. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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