



ORIGINAL ARTICLE

EFFECT OF TWO *LIMOSILACTOBACILLUS* STRAINS AND *SALMONELLA* CHALLENGE ON IMMUNE MARKERS IN A POULTRY CAECAL MODELZuzana Kiššová^{1*}, Veronika Vinclérová¹, Csilla Tóthová², Viera Karaffová¹¹Department of Morphological Disciplines, University of Veterinary Medicine and Pharmacy in Košice, Košice, Slovak Republic; ²University Veterinary Hospital, Clinic of Ruminants, University of Veterinary Medicine and Pharmacy in Košice, Košice, Slovak Republic

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Ethical considerations: When reporting experiments on animals Observation of the ARRIVE guidelines 2.0: Updated guidelines for reporting animal research, published on July 14, 2020 (DOI: [10.1371/journal.pbio.3000410](https://doi.org/10.1371/journal.pbio.3000410)), is applied. The authors ensure that all procedures were performed in compliance with the guidelines for animal care of their institutions or with national/international guidelines.

ABSTRACT

Probiotic microorganisms are increasingly investigated for their capacity to influence host physiology, particularly through interactions with the intestinal immune system. The present study aimed to assess the effects of selected probiotic strains, *Limosilactobacillus reuteri* CCM 9425 and *Limosilactobacillus reuteri* B2/6, applied simultaneously in an *ex vivo* model of poultry caecal explants, with a focus on their impact on immune-related gene expression. In addition to probiotic treatment, explants were challenged with *Salmonella* Enteritidis PT4 to evaluate immune responses under infectious conditions and following probiotic pre-treatment. The transcriptional profiles of selected cytokines (IL-15, IL-1 β , IL-8, and IL-18) indicated that probiotic exposure did not trigger an exaggerated inflammatory response. Instead, a consistent and significant increase in IL-15 expression was observed in both the probiotic-treated group and the group receiving probiotic pre-treatment ($p < 0.01$). The upregulation of IL-15, a cytokine involved in early immune defense and activation of innate immune cells, may reflect enhanced immune readiness without accompanying tissue damage. Taken together, these findings demonstrate that the investigated probiotic strains can modulate intestinal immune responses in a controlled manner, supporting gut homeostasis while avoiding harmful inflammation.

Keywords: caecal explants; cytokines, gut immunity; probiotics; *Salmonella* Enteritidis

INTRODUCTION

Probiotic bacterial strains are widely recognized for their beneficial effects on both human and animal health. Numerous studies highlight the importance of lactic acid

bacteria (LAB) not only for the intestinal environment and digestion but also for the overall condition of the organism, including immunity, behavior, and the nervous system [1]. Their relevance is particularly pronounced in the context of the emerging post-antibiotic era, in which

the use of antimicrobial treatments should be strictly limited to necessary cases. However, in practice, antibiotics are often used excessively and unjustifiably, not only in livestock production but also in human medicine, thereby contributing to the spread of antimicrobial resistance [2]. Probiotics and other natural substances therefore represent a promising strategy for supporting gut health and the immune system. At the same time, there is increasing emphasis on the protection of experimental animals due to stricter legislation and growing societal awareness [3]. Despite this, the study of zoonotic pathogens in poultry still frequently relies on murine *in vivo* models or heterologous *in vitro* systems, which exhibit significant limitations due to the species-specific nature of host–pathogen interactions [4]. The replication capacity and infectivity of many microorganisms are closely linked to a specific host, which reduces the relevance of the obtained results. Moreover, research on the poultry gastrointestinal tract is limited by the lack of suitable cellular models, as available epithelial cell lines fail to reproduce the complex cellular heterogeneity and full functionality of intestinal tissue [5]. For this reason, alternative experimental approaches are currently being intensively developed, particularly *ex vivo* and advanced *in vitro* models, which allow for a better simulation of *in vivo* physiological conditions and provide more relevant results in the study of gut health, immunity, and host–microorganism interactions [4].

In the present study, we focused on the isolation and experimental use of the poultry caecum to investigate the immunomodulatory potential of the probiotic strain *Limosilactobacillus reuteri* CCM 9425 in combination with *Limosilactobacillus reuteri* B2/6 alone and in combination with experimental infection induced by the pathogenic strain *Salmonella* Enteritidis PT4. Our previous studies demonstrated good reproducibility and applicability of an ileal explant model derived from the poultry intestine [6, 7]. The cecum represents a highly specialized part of the digestive tract with an important role in microbial fermentation, immune processes, and water absorption.

MATERIAL AND METHODS

Isolation of caecal explant cultures

Sample isolation was performed according to the procedure described in our previous study [7]. Briefly, Ross

308 poultry (one 21-day-old female) was humanely euthanized by decapitation following prior anesthesia with carbon dioxide (CO₂). After opening the coelomic cavity, the caecal portion of the intestine was collected. Intestinal explants from the cecum were obtained using reusable biopsy punches with plungers. Bacterial cultivation: The probiotic strains *Limosilactobacillus reuteri* CCM 9425 and *Limosilactobacillus reuteri* B2/6 (PP) were isolated from the intestinal contents of healthy pheasants at the Department of Microbiology and Immunology (University of Veterinary Medicine and Pharmacy in Košice, Slovakia). The strains were cultivated in de Man, Rogosa, and Sharpe (MRS) broth (Merck) at 37 °C overnight under static conditions. *Salmonella enterica* serovar Enteritidis (S. Enteritidis; SE), phage type PT4 (Veterinary Research Institute, Brno, Czech Republic), was cultured in Luria–Bertani broth (LB; Sigma-Aldrich, St. Louis, MO, USA) overnight at 37 °C with continuous shaking (160 rpm). Overnight cultures were subsequently inoculated into fresh LB broth and incubated for 4 hours at 37 °C with constant agitation. Prior to the experiments, bacterial concentrations were quantified by measuring optical density at 600 nm, according to the procedure described by Kiššová et al. (2025) [6].

Experimental design

The experimental setup and the distribution of individual experimental groups are presented in Table 1. Following the indicated treatments, explants from all experimental groups were incubated for an additional 1 h in medium supplemented with 100 µg/mL gentamicin (Sigma-Aldrich, St. Louis, MO, USA) to eliminate any remaining extracellular bacteria and ensure identical treatment conditions across all groups.

Analysis of relative gene expression

The total RNA from each sample was isolated from the explants using the RNeasy Mini Kit (Qiagen, Hilden, Germany) exactly according to the manufacturer's instructions. The quantity and purity of RNA (free of DNA and proteins) were determined at 260/280 nm, using NanoDrop 8000 (Thermo Scientific, Waltham, MA, USA). The cDNA was reverse-transcribed from RNA, using the iScript cDNA Synthesis kit (Bio-Rad, Hercules, CA, USA) as outlined by the manufacturer. The qPCR analysis was performed using the CFX96 Touch Real-Time PCR Detection System (Bio-Rad, USA) in a 10 µL reaction volume

Table 1. Experimental scheme of the treated ceecal explant cultures

Experimental group	Type of treatment	Application of Gentamicin 100 ug/mL/1h	Abbreviation
Control	Without treatment	✓	-
Probiotic group	Simultaneous application of <i>L. reuteri</i> CCM 9425 and <i>L. reuteri</i> B2/6, each at a concentration of 5×10^7 CFU/mL (2 h; 37 °C).	✓	PP
Infection group	Infection with SE at a concentration of 10^7 CFU/mL (2 h; 37°C)	✓	S
Pre-treatment group	Pre-treatment with simultaneous application of <i>L. reuteri</i> CCM 9425 and <i>L. reuteri</i> B2/6, each at a concentration of 5×10^7 CFU/mL (2 h; 37 °C) and subsequent infection with SE at a concentration of 10^7 CFU/mL (2 h; 37°C)	✓	PP+S

The table describes each type of treatment applied in the individual experimental groups.

containing $1 \times iQ^{\text{TM}}$ SYBR® Green Supermix (Bio-Rad), 0.5 µM forward and reverse primers, and 40 ng/µL of cDNA. Ubiquitin was used as a reference gene for internal control. All reactions were performed in triplicate. The experimental protocol consisted of the initial denaturation at 95 °C for 5 min, followed by amplification – 40 cycles of 3 steps (denaturation at 94 °C for 30 s, annealing at 60 °C for 30 s, extension at 72 °C for 30 s), and final extension at 72 °C for 15 min, followed by melting curve analysis to confirm the amplification of a specific product. Relative normalized expression was calculated using the $2^{-\Delta\Delta CT}$ method. Results of the gene expression experiment conducted in triplicate were expressed as mean $\pm$ standard deviation (SD). Primers for the mRNA expression analysis are listed in Table 2.

Statistics

Significant differences in gene expression analyses were determined in GraphPad Prism 9.0.0 software (GraphPad Software Inc., San Diego, USA) by one-way analysis of variance (ANOVA) followed by Dunnett's

multiple comparisons. The level of significance was set as P-value ≤ 0.05 considered significant (*), P-value ≤ 0.01 considered highly significant (**), P-value ≤ 0.001 (***) considered very highly significant.

RESULTS

The aim of the present study was to evaluate the immunomodulatory potential of simultaneously applied LAB strains and their prospective protective effect in a model infection with *Salmonella* Enteritidis using an *ex vivo* model of poultry caecal explants.

Caecal explants were isolated using 4 mm biopsy needles, and the obtained tissue punch samples were subsequently placed into a 96-well plate containing DMEM/F12 medium supplemented with growth factors (Figure 1). The use of this standardized isolation approach enabled the preparation of uniform explants and ensured consistent experimental conditions across all samples.

Table 2. Table of used primers

Gene name	Abbreviation	Primer sequence 5'→3'	Reference
Interleukin-18	IL-18	F: ACGTGGCAGCTTTTGAAGAT R: GCGGTGGTTTTGTAAACAGTG	[8]
Interleukin-8	IL-8	F: ATGAACGGCAAGCTTGGAGCT R: GCAGCTCATTCCTTCCATCTT	[8]
Interleukin-15	IL-15	F: TGGAGCTGATCAAGACATCTG R: CATTACAGGTTCTTGGCATTCT	[9]
Interleukin-1 beta	IL-1β	F: GAAGTGCTTCGTGCTGGAGT R: ACTGGCATCTGCCAGTTC	[8]
Ubiquitin	UB	F: GGATGCAGATCTTCGTGAAA R: CTTGCCAGCAAAGATCAACCTT	[10]
Glyceraldehyde 3-phosphate dehydrogenase	GAPDH	F: GGCACGCCATCACTATC R: CCTGCATCTGCCATTT	[10]



Fig. 1. Isolation of explants

Representative image of explant isolation from the poultry intestine.

The main finding was that the application of probiotics, either alone or in the experimental group referred to as the pre-treatment group, where caecal explants were pre-treated with both lactobacilli strains during a 2-hour incubation and subsequently exposed to infection with the pathogen *S. Enteritidis* did not lead to an increased expression of the monitored pro-inflammatory cytokines such as IL-1 β , IL-8, and IL-18 (Fig. 2).

However, a significant upregulation was observed in mRNA encoding the cytokine IL-15, both in the probiotic group ($p < 0.01$) and in the pre-treatment group ($p < 0.01$) compared to the control group (Fig. 2). Conversely, in the infection group, where intestinal inflammation was induced by the pathogenic strain *S. Enteritidis*, an increased expression of genes encoding IL-8 ($p < 0.001$) and IL-1 β ($p < 0.05$) was detected.

DISCUSSION

The absence of increased expression of conventional pro-inflammatory cytokines suggests that the applied combination of LAB does not induce an excessive inflammatory response in intestinal tissue. This aspect is particularly important, as uncontrolled inflammation may lead to epithelial damage and disruption of the intestinal barrier [11, 12]. In addition to preventing tissue injury, the maintenance of a balanced inflammatory tone is essential for pre-

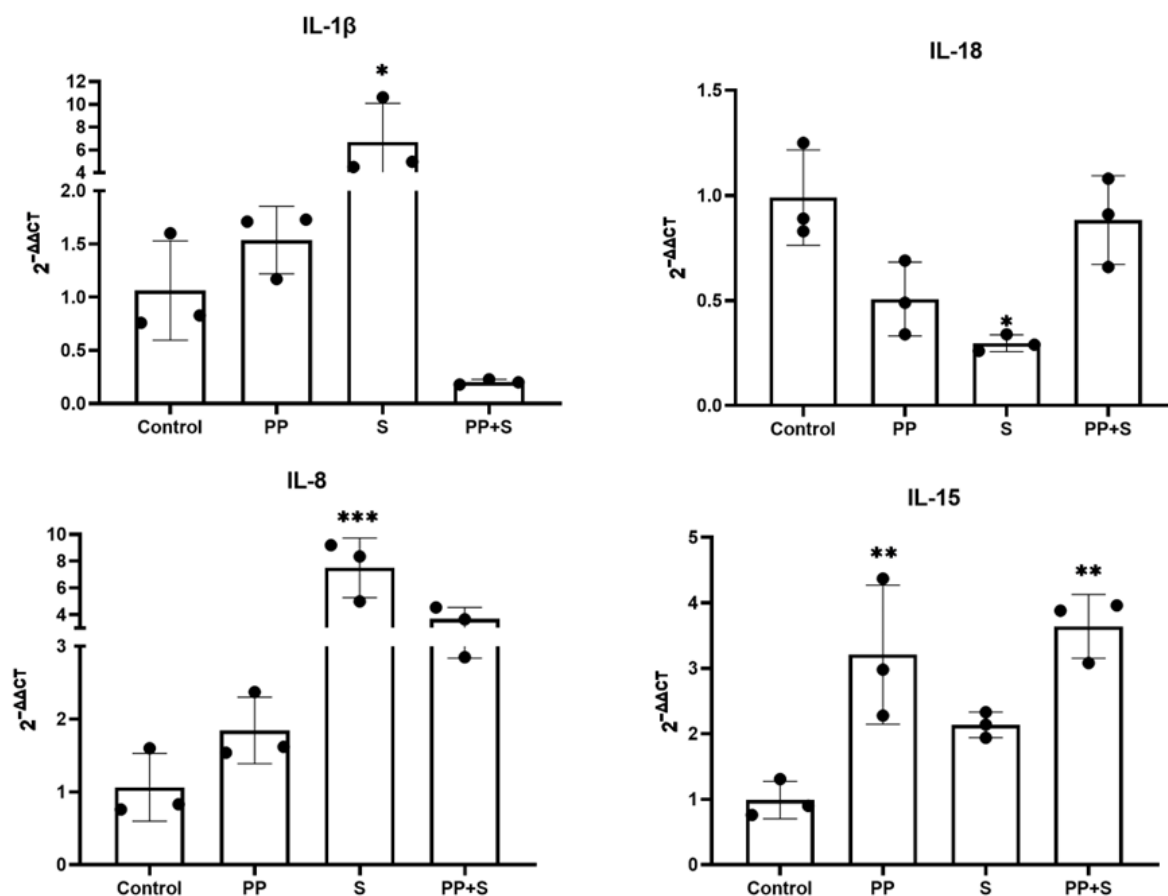


Fig. 2. Gene expression analysis

Results are expressed as mean $\pm$ SD ($n = 6$). Statistical significance of differences was assessed using Dunnett's multiple comparison test. Results were significantly different compared to the control experimental group at statistical significance levels (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

serving epithelial integrity and proper nutrient absorption. Similar findings have been reported in previous studies, where probiotic bacteria, particularly strains of *Limosilactobacillus reuteri*, demonstrated the ability to modulate immune responses without inducing strong pro-inflammatory signaling [13, 14]. These observations support the concept that probiotics can fine-tune host immunity rather than simply activating or suppressing it.

Notably, a significant upregulation of IL-15 was observed in probiotic-treated groups. IL-15 plays a key role in the activation and proliferation of NK cells and memory CD8⁺ T lymphocytes and is crucial for early phases of mucosal immunity [15, 16]. Moreover, IL-15 is involved in the maintenance of intraepithelial lymphocytes, which are essential for epithelial surveillance and rapid immune responses at mucosal surfaces. The increased expression of IL-15 may therefore indicate that probiotic application does not trigger inflammation but rather “primes” the immune system for a more effective response against pathogens. This effect aligns with the concept of immunological priming, where host readiness is enhanced without tissue damage [16]. Such priming may be particularly advantageous in production animals, where rapid responses to enteric pathogens are critical for maintaining health and performance.

In the context of *Salmonella* infection, it is particularly noteworthy that even in the pre-treated experimental group, no increase in the expression of genes encoding IL-1 β , IL-18, and IL-8 was observed. These cytokines are typically associated with inflammasome activation and neutrophil recruitment during bacterial infections [17, 18]. Although infection with the pathogenic strain *S. Enteritidis* was confirmed by increased expression of mRNA encoding genes such as IL-1 β , IL-8, and IL-15, similar findings were observed in our previous study using a porcine epithelial cell line, where infection with *Salmonella Typhimurium* resulted in elevated expression of pro-inflammatory cytokines such as TNF- α , IL-8, and IL-6 [19]. The unchanged expression in pre-treated probiotic group suggests that probiotic pre-treatment may prevent excessive activation of innate immune pathways that are often linked to tissue damage. Therefore, our results indicate that LAB may attenuate pathogen-induced inflammatory responses while still allowing the activation of protective immune mechanisms. This selective modulation of the immune response could represent a key advantage of probiotic application over conventional antimicrobial strategies.

This effect may be mediated by several mechanisms, including competitive exclusion of the pathogen, inhibition of its adhesion to epithelial cells, or modulation of host signaling pathways such as NF- κ B and MAPK [20]. In addition, probiotic-derived metabolites, including short-chain fatty acids and bacteriocins, may contribute to the suppression of pathogen growth and virulence [21].

The intestinal explant model represents a suitable *ex vivo* system that preserves the complex architecture of intestinal tissue, including epithelial and resident immune cells, thereby providing more physiologically relevant results compared to conventional *in vitro* models. This model allows for the investigation of host–microbe interactions in a controlled environment while retaining key structural and functional features of the intestine [22]. However, due to its complex microbiota and dominant immune tolerance mechanisms, it remains questionable whether it is an optimal model for studying early host–pathogen interactions. Future studies may benefit from combining explant models with simplified systems or microbiota-controlled conditions to better dissect the initial stages of infection and immune activation.

CONCLUSION

Our findings suggest that the probiotics used in this study are capable of subtly modulating the intestinal immune response without triggering an undesirable pro-inflammatory reaction. At the same time, this type of immune modulation contributes to the maintenance of intestinal homeostasis and supports the integrity of the gut environment. Moreover, the results demonstrate the suitability of the chicken intestinal explant model as a valuable *ex vivo* platform for the initial screening of probiotic immunomodulatory properties before *in vivo* validation.

Data Availability Statement

The raw data of this article will be made available by the authors, without undue reservation.

Ethical Statement

This study was performed in accordance with the guidelines for animal welfare and was approved by the

Ethics Committee for the approval of research involving animals by the legislative requirements applicable at the UVMP in Košice with permit No. EKVP/2025–05.

Conflict of Interest

The authors declare no competing interests.

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Generative AI Statement

There were no generative AI and AI-assisted technologies used in writing the manuscript. All scientific content, interpretation, and conclusions remain the responsibility of the author. AI-based language model were used only to assist with English language editing and grammar correction. The authors reviewed and approved all modifications and take full responsibility for the final content.

Authors' Contributions

Conceptualization, ZK, VK, and VV. Methodology, ZK, VV, VK and CT. Data curation, ZK, VK, and VV. Formal analysis, writing – original draft preparation, ZK, VV and CT. Supervision, VK. The cell cultures were prepared by VV, and VK. Writing – review and editing, ZK. The management for research activity planning and the financial support for the project leading to this publication were performed by VK and ZK. All authors have read and agreed to the published version of the manuscript.

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