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Temperature-Dependent Modulation of *Yeni and Yenr* Quorum Sensing Gene Expression in *Yersinia Enterocolitica* by Probiotic *Bifidobacterium* Species

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Abstract

Background and Objective: The process of coordination and communication between cells through diffusible signaling molecules is known as quorum sensing. Quorum sensing affects several factors in pathogens, including pathogenicity, adhesion, motility, biofilm production and cell aggregation. By controlling these signaling molecules, pathogenic factors can be controlled.

Material and Methods: In this study, effects of *Bifidobacterium lactis*, *Bifidobacterium bifidum* and *Bifidobacterium longum* on the expression of quorum sensing genes in *Yersinia enterocolitica* were studied at two various temperatures of 37 and 32 °C. First, *Bifidobacterium* spp. were activated in brain infusion broth and then cultured simultaneously with *Yersinia enterocolitica*, RNA extraction was carried out and *yen*I and *yen*R gene expression was assessed using real-time polymerase chain reaction.

Results and Conclusion: Results revealed significant differences in gene expression at 37 and 32 °C. When *Bifidobacterium* sp. was co-cultured with *Yersinia enterocolitica* at 32 °C, the bacterial quorum sensing gene expression significantly decreased in all treated cells, except *yen*I in *Bifidobacterium bifidum* co-culture, compared to the control. *Bifidobacterium longum* showed the highest decreasing effect in quorum sensing gene expression in *Yersinia* sp. by 64%. In contrast, co-culturing *Bifidobacterium* sp. with *Yersinia enterocolitica* at 37 °C revealed that Quorum sensing gene expression levels in *Yersinia enterocolitica* did was not change significantly in all cultures, except that with *Bifidobacterium bifidum*; almost similar to the control samples. These findings indicated that the interactions between probiotic bacteria and pathogens varied under various temperature conditions, demonstrating a temperature-dependent pattern.

Keywords: *Bifidobacterium* spp., Gene expression, Gene regulation, Quorum sensing, *Yersinia enterocolitica*

What is "already known" on this topic:

- Quorum sensing (QS) is a key mechanism in Gram-negative bacteria like *Yersinia enterocolitica* that regulates virulence factors such as biofilm formation, motility, and adhesion through AHL-mediated signaling systems.
- The *yenI/yenR* system in *Y. enterocolitica* produces and regulates specific AHL signals (C6-HSL and 3-oxo-C6-HSL), playing a critical role in QS regulation unique to this species.
- Certain probiotics, such as *Bifidobacterium longum*, have shown potential to inhibit QS-related pathogenicity and gene expression in bacteria like *E. coli* and *P. aeruginosa* through various mechanisms.

What this article adds:	➢ Demonstrates for the first time that *Bifidobacterium spp.* can reduce *yenI* and *yenR* quorum sensing gene expression in *Y. enterocolitica*, with the strongest inhibition seen in co-culture with *B. longum* at 32°C. ➢ Reveals a temperature-dependent interaction between probiotics and *Y. enterocolitica*, where QS gene suppression is significant at 32°C but largely absent at 37°C. ➢ Highlights the potential of probiotic-based interventions in controlling QS-regulated virulence in foodborne pathogens under specific environmental conditions.

1. Introduction

Quorum sensing (QS) refers to the process of coordination and communication between cells, involving production of diffusible extracellular molecules and hence regulation of specific gene expression. The QS signals are called autoinducers because they are produced by the cells and typically induce their own synthesis, creating a positive feedback loop. Various types of QS systems reported in microorganisms include 1) LuxI/R type, which is commonly used by Gram-negative bacteria and uses acyl-homoserine lactone (AHL) molecules. This system is used for intraspecies communication due to its high specificity; 2) peptide signaling system, used by Gram-positive bacteria; 3) AI-2/LuxS signaling system, which facilitates interspecies communication and is detected in all bacteria and 4) AI-3 signaling system, which operates through epinephrine-norepinephrine and is used for interspecies and interterritorial communications [1,2,3]. In Gram-negative bacteria, QS can be inhibited through three methods of 1) inhibiting synthesis of AHLs, 2) degrading AHL molecules and 3) interfering with the receptors, which can be achieved through compounds produced by plants and microorganisms [4].

Yersinia enterocolitica, as a member of the Enterobacteriaceae family, is a Gram-negative, short rod-shaped, facultative anaerobic non-spore-forming bacterium. It multiplies at 0–45 °C, which distinguishes it from other enteric pathogenic bacteria [5]. Studies have shown that the three pathogenic species of *Yersinia* produce AHLs QS signals. Protein of LuxI, which synthesizes AHL as well as LuxR as a regulator, is detected in all three pathogenic *Yersinia* spp. However, *Y. enterocolitica* includes a unique pair of LuxRI *(*YenRI*)*, whereas the other two species include two pairs. The YenI is responsible for synthesizing two types of AHLs, one of which is N-hexanoyl homoserine lactone (C6-HSL) and the other is N-3-oxo-hexanoyl homoserine lactone (3-OXO-C6-HSL). These two compounds are produced at a 1:1 ratio in *Y. enterocolitica* [6,7,8].

Gut microflora of humans and animals consists of several probiotic species such as *Bifidobacterium*. Typically, population of *Bifidobacterium* in the intestine of healthy adults ranges 10^{10}-10^{11} CFU g^{-1}; however, this decreases with age. Most species of *Bifidobacterium* are rod-shaped, anaerobic, non-motile and non-spore-forming species. Dairy fermentation products such as yogurt, cheese and fermented butter are addressed as major sources of probiotics [9]. For QS inhibition, extensive studies have been carried out on various pathogenic bacteria. In one study carried out on bacteria isolated from fish, 200 bacterial species were isolated from fish and ability of three selected species to inhibit QS system in *Aeromonas hydrophila* was verified. The study revealed that the bacteria belonged to the *Bacillus* genus and possessed an enzyme capable of degrading AHLs. The effect of this bacterium on *A. hydrophila* in fish showed that the control group of fish developed skin lesions over time and died after 12 d. However, fish that consumed the isolated strain survived and skin damage significantly decreased [10]. In another study investigating the effect of stress on signal production in *Listeria* spp., it was reported that stress induced by nisin and lactic acid did not play a role in production of AI-2 as an adaptive response to the environment and no dependency between these two factors was observed. However, this study concluded that QS could generally help *L. monocytogenes* cells adapted to stresses such as nisin and lactic acid [11].

Further studies on the inhibitory effect of various *Bifidobacterium* strains on EHEC (Enterohemorrhagic *Escherichia coli)* showed that *B. longum*, *B. adolescentis* and *B. breve* were the most inhibitory strains. For biofilm formation, most *Bifidobacterium* strains did not show a significant inhibitory effect, with only *B. longum* decreasing biofilm formation by 36%. Pathogenicity decreased in the presence of *B. longum* and results indicated that it regulated seven types of proteins in *Escherichia coli* [12]. Study of the effect of lactic acid produced by *Pediococcus acetilactis* on QS in *Pseudomonas aeruginosa* showed that lactic acid included an inhibitory effect on motility and short-chain HSL, elastase, protease, pyocyanin and biofilm productions. However, concentration of lactic acid needed to be precisely

assessed for effective QS regulation [13]. Generally, the present study aimed to investigate the effect of co-culturing *B. lactis*, *B. bifidum* and *B. longum* on the expression of QS genes, *yen*I and *yen*R, in *Y. enterocolitica* under various temperature conditions.

2. Materials and Methods

2.1. Bacterial Strain Preparation and Activation

The bacterial strains of *B. lactis* ATCC 19435, *B. bifidum* ATCC 29521, *B. longum* ATCC 15707 and *Y. enterocolitica* ATCC 23715 were provided by the Iranian Research Organization for Science and Technology (IROST). The *Bifidobacterium* strains were cultured in brain heart infusion (BHI) media (Merck, Germany) at 37 °C for 48 h under absolute anaerobic conditions using type A gas pack, anaerobic jar and indicators. Moreover, *Y. enterocolitica* was cultured in BHI media at 29 °C for 48 h [12]. For co-culturing *Bifidobacterium* spp. with *Y. enterocolitica*, fresh 24-h cultures of each *Bifidobacterium* strain were first adjusted to a cell density of 0.5 McFarland standard. Then, 100 µl of each adjusted *Bifidobacterium* culture were added to 10 ml of fresh *Y. enterocolitica* culture media and incubated at the specified temperature for each treatment [12].

2.2. Simultaneous Cultivation of *Bifidobacterium* sp. with *Yersinia enterocolitica*

The *Y. enterocolitica* was cultured in BHI media with three various probiotic bacteria separately at 32 and 37 °C for 48 h under anaerobic conditions. To standardize cell populations and ensure addition of a consistent microbial cell count in the assays, 0.5 McFarland standard was used with fresh 24-h culture that experienced two previous passages [12].

2.3. Primer Design and Polymerase Chain Reaction for the Verification of *yen*I and *yen*R Gene Presence

Primers were designed for the analysis of *yen*I and *Yen*R genes as well as the housekeeping gene (Table 1). Briefly, DNA extraction from *Y. enterocolitica* was carried out using boiling method. Then, polymerase chain reaction (PCR) was carried out (ASTEC G02, Japan) and the PCR products were analyzed via gel electrophoresis.

2.4. RNA Extraction and Reverse-transcriptase Polymerase Chain Reaction Analysis

Yersinia enterocolitica and each *Bifidobacterium* sp. were simultaneously incubated at 32 and 37 °C for 48 h under anaerobic conditions. After incubation, cultures were centrifuged and the supernatant was discarded. The cell pellet was collected using 1.5-ml microtubes for RNA extraction. The RNA extraction was carried out using extraction kit (Kiagen Fanavar Arya, Iran) based on the manufacturer's instructions and the RNA concentration was assessed using NanoDrop spectrophotometer (Thermo Scientific NanoDrop 2000, USA). Furthermore, cDNA synthesis was carried out using cDNA synthesis kit (Yekta Tajhiz Azma, Iran) and gene expression analysis was carried out using reverse-transcriptase polymerase chain reaction (RT-PCR) machine (Corbett Rotor Gene-RG 3000, Australia). Gene expression was analyzed using 2^-ΔΔCt method [14]. This method involved assessing gene expression level and normalizing it against a reference gene. Normalization corrected for variations in amplification efficiency, extraction conditions and initial sample volumes. Gene expression levels in treated and untreated samples were investigated and the difference in Ct values was calculated. Similar procedure was used to the reference sample. The relative gene expression changes were calculated by dividing the gene expression changes in the target gene by those of the reference gene. The calculation method and formulas were as follows [15]:

$$\Delta Ct = Ct_{\text{target gene}} - Ct_{\text{housekeeping gene}},\ \Delta\Delta Ct = \Delta Ct_{\text{experiment}} - \Delta Ct_{\text{Control}},\ \text{Fold gene} = 2^{-\Delta\Delta Ct}$$

Where, Ct was the threshold cycle.

2.5. Statistical analysis

The mean Ct values of the treated samples were compared to those of the controls using one-way analysis of variance (ANOVA) to investigate if there was a statically significant difference between them ($p < 0.05$). All experiments were carried out in triplicate.

Table 1: List of primers designed to examine the expression of *Yen I* and *Yen R* genes

Name	Sequence (5' → 3')
Yen I	F=TTGCCCACCATATCTCTT
	R=TCCAGCCGATTCTTTGTT
Yen R	F=CCTCTGCATCCCACTATT
	R=ACTTTATCTTTCGCCGTC
16S	F=CCCAACATTTCACAACAC
	R=ACCTTACCTACTCTTGAC

3. Results and Discussion

3.1. Verification of the presence of *yen*I and *yen*R genes in *Yersinia enterocolitica*

First, presence of the *yen*I and *yen*R genes in *Y. enterocolitica* strain must be verified. Results of the PCR amplification of *yen*I and *yen*R genes in *Y. enterocolitica* and their verification on agarose gels are shown in Figures 1 and 2. Figure 1 verified presence of the *yen*I gene and Figure 2 verified presence of the *yen*R gene.

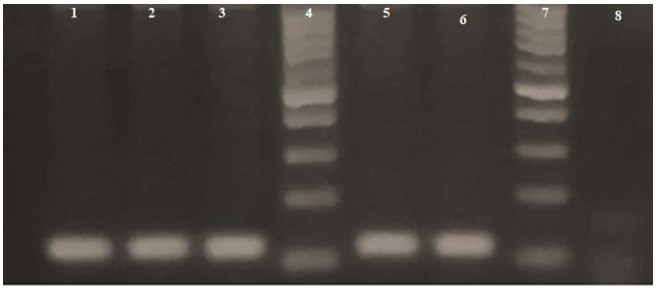

Figure 1: Gel agarose image for the confirmation of the *Yen I* gene presence, negative Control(8), Sample (1, 2, 3, 5 and 6), ladder (4 and 7) Target gene length 50bp

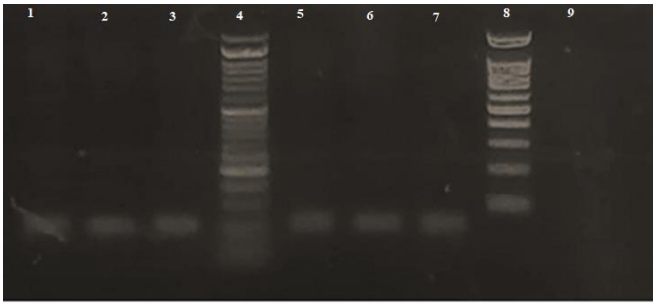

Figure 2: Gel agarose image for the confirmation of the *Yen R* gene presence, negative Control(9), Sample (1, 2, 3, 5, 6and7), ladder (4 and 8) Target gene length 110bp

3.2. Analysis of *yen*I and *yen*R gene expression in *Yersinia enterocolitica* co-cultured with *Bifidobacterium* strains at 37 and 32 °C

The T-PCR analysis results Fold change for the *yen*I and *yen*R genes in comparison to the housekeeping gene are shown in Tables 2 and 3 and Figures 3 and 4. Fold change is a metric that expresses the extent of change between two measurements. In gene expression analysis, such as microarray or RNA-Seq analysis, it refers to the ratio of expression between samples or between groups. Moreover, melting curve and amplification of the target sequence in the treatments during RT-PCR are shown in Figure 5. In results achieved at 32 °C, adding *Bifidobacterium* to *Y. enterocolitica* culture decreased QS gene expression. At 37 °C, results completely varied. Results showed differences in expression of the studied genes at 37 and 32 °C. At 32 °C, presence of *Bifidobacterium* sp. decreased the expression of signal-producing genes, which was significant in most samples. At 37 °C unlike 32 °C, most samples did not differ significantly from the control samples. Studies have shown that 37 °C significantly affects regulation of genes associated to pathogenesis such as secretion systems and toxins and helps bacteria multiply better in host conditions.

In *Y. enterocolitica*, gene expression was affected by temperature, particularly at 37 °C. These temperature-dependent changes in gene expression assisted the bacteria effectively evaded the host immune system and enhanced its virulence. Specifically, at this temperature, expression of key genes associated with the bacterial virulence factors increased. These genes included those involved in the secretion of specific proteins, toxin production and responses to environmental stresses. At 37 °C, *Y. enterocolitica* efficiently used type III secretion system (T3SS), which was essential for the transfer of toxic proteins into host cells and expression of genes linked to this system increased significantly. Genes involved in production of specific toxins that helped in the bacterial toxic activities and proteins that prevented the host cell's immune responses and regulatory systems for survival and stress conditions were significantly upregulated [16-18].

Table 2: Real-time PCR analysis results of *Yen I* and *Yen R* gene expression in *Yersinia enterocolitica* co-cultured with *Bifidobacteriuml* strains at 32°C, based on Ct values

Treatment	Genes	Ct, average
Control	House keeping	20.75 ± 0.335 [a*]
	Gene I	25.19 ± 0.187 [a]
	Gene R	24.83 ± 0.537 [a]
B. lactis + Y. enterocolitica	House keeping	20.18 ± 0.331 [a]
	Gene I	25.75 ± 0.377 [b]
	Gene R	25.75 ± 0.124 [b]
B. longum + Y. enterocolitica	House keeping	20.38 ± 0.496 [a]
	Gene I	25.72 ± 0.337 [b]
	Gene R	25.62 ± 0.186 [b]
B. bifidum + Y. enterocolitica	House keeping	21.57 ± 0.334 [a]
	Gene I	26.35 ± 0.306 [a]
	Gene R	26.76 ± 0.443 [b]

[*] Mean values with different superscript letters (a, b) differ significantly from the control group ($p < 0.05$), while mean values sharing the same letter show no significant difference ($p > 0.05$) compared to the control

Table 3: Real-time PCR analysis results of *Yen I* and *Yen R* gene expression in *Yersinia enterocolitica* co-cultured with *Bifidobacteriuml* strains at 37°C, based on Ct values.

Treatment	Genes	Ct average
Control	House keeping	22.085±0.415[a]
	Gene I	25.928±0.466[a]
	Gene R	25.173±0.206[a]
B. lactis + Y. enterocolitica	House keeping	24.343±0.351[a]
	Gene I	25.504±0.622[a]
	Gene R	26.635±1.369[a]
B. longum + Y. enterocolitica	House keeping	20.873±2.857[a]
	Gene I	26.285±0.847[a]
	Gene R	26.334±1.267[a]
B. bifidum + Y. enterocolitica	House keeping	26.443±0.669[a]
	Gene I	28.15±0.829[b]
	Gene R	27.788±0.411[b]

* Mean values with different superscript letters (a, b) differ significantly from the control group ($p < 0.05$), while mean values sharing the same letter show no significant difference ($p > 0.05$) compared to the control

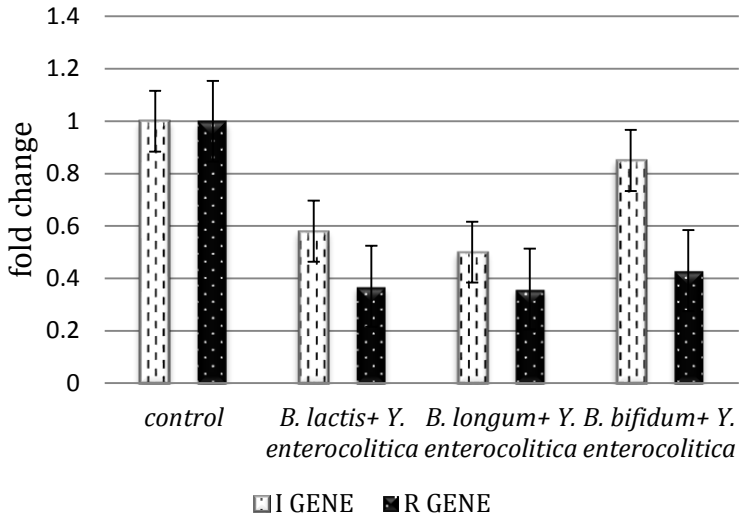

Figure 3: Comparative analysis of *YenI* and *YenR* gene expression in *Yersinia enterocolitica* at 32°C following co-culture with various *Bifidobacterium* strains, as determined by RT-qPCR. Data are presented as fold change relative to the untreated control group.

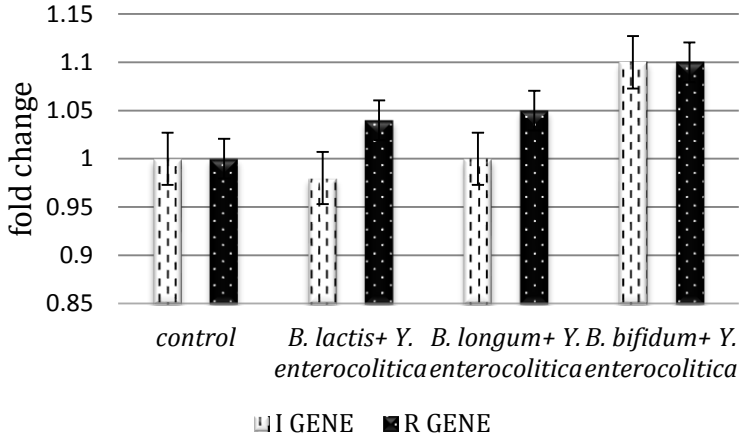

Figure 4: Comparative analysis of *YenI* and *YenR* gene expression in *Yersinia enterocolitica* at 37°C following co-culture with various *Bifidobacterium* strains, as determined by RT-qPCR. Data are presented as fold change relative to the untreated control group.

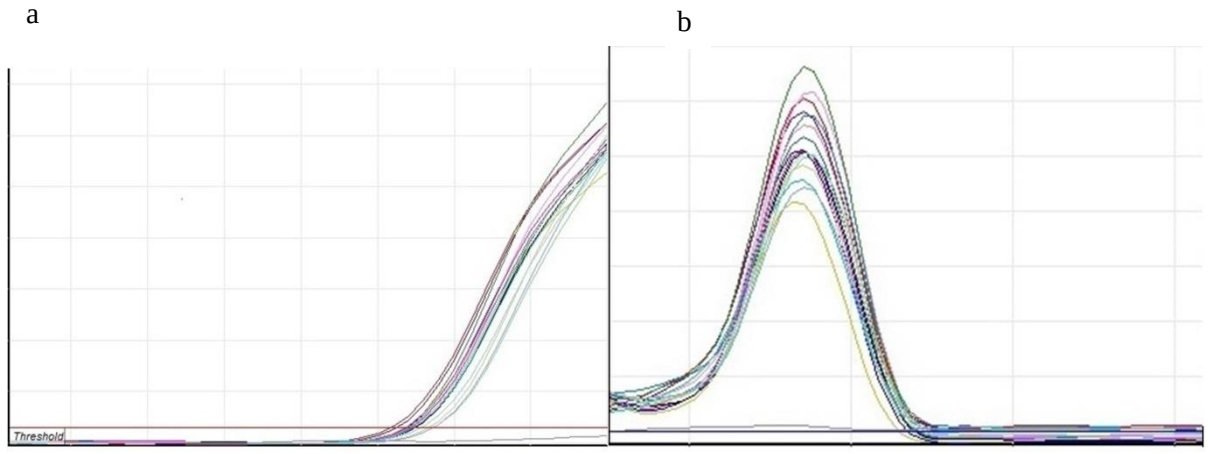

Figure 5: Melting curve analysis of RT-qPCR amplification products. (a) Amplification plots showing exponential phase and plateau for target sequences. (b) Single-peak melting curves confirm specific amplification, with no evidence of primer-dimers or non-specific products. The consistent Tm values across replicates validate reaction specificity and data reliability

.

Technically, *Y. enterocolitica*, genes responsible for the production of AHLs can be regulated in response to environmental changes and host conditions [8]. Studies have shown that at 37 °C as the natural body temperature of humans, changes in the expression of these genes occur. Compounds encoded by these genes are involved in regulating collective behaviors such as toxin production, biofilm formation, pathogen-linked behaviors, host interactions and responses to environmental stress. At 37 °C, AHL production may increase, as this temperature specifically mimics the natural conditions of the human body and is critical for regulating pathogenic activities of the bacteria. Therefore, AHL-producing genes may become more active at this temperature, enabling the bacteria to regulate their collective behaviors, including toxin production and expression of other virulence factors [19, 20].

Naturally, *Y. enterocolitica* is an enteric pathogen that grows rapidly at 37 °C. At 37 °C, *Y. enterocolitica* typically reaches its maximum growth within 6–12 h, while bifidobacteria needs 12–24 h. Due to their high sensitivity to environmental conditions, bifidobacteria grow more slowly than that *Y. enterocolitica* does at 37 °C. Since *Y. enterocolitica* grows faster and reaches higher numbers within a shorter time at 37 °C compared to bifidobacteria, and due to the increases in expression of signal-producing genes involved in QS, toxin production, biofilm formation, pathogenic behavior and host interaction, it seems that *Y. enterocolitica* proliferates sufficiently and produces necessary beneficial compounds before bifidobacteria can reach sufficient numbers and begin production of inhibitory compounds. Additionally, these compounds (e.g. acidic substances) may further inhibit rapid growth of bifidobacteria. Once *Y. enterocolitica* dominates the environment, bifidobacterial growth becomes restricted. Due to the high sensitivity of bifidobacteria to environmental compounds, there is a possibility of no or weak growth of these bacteria. Secreted compounds needed for the bifidobacterial growth at 37 °C may be used by *Y. enterocolitica* due to the high number of *Y. enterocolitica* in the environment; thus, accelerating the bacterial growth [21,22,23].

In contrast, growth dynamics of the two bacterial species differ at 32 °C under strict anaerobic conditions, with bifidobacteria growing slightly faster than *Y. enterocolitica*. This faster growth of bifidobacteria leads to the production of growth-inhibitory compounds, limiting *Y. enterocolitica* proliferation and hence affecting expression of QS genes. At this temperature, expression of QS genes is less than that at 37 °C, as pathogenic activity is optimal at the latter temperature [24,25]. Based on these findings, presence of significant differences in the expression of QS genes at 32 °C and absence of significant differences of these genes at 37 °C can be justified. At the two temperatures, *B. longum* showed the minimum gene expression averagely. Previous studies on *B. longum* have shown that this bacterium is a clinically versatile probiotic strain and can control growth of pathogenic bacteria [26,27].

4. Conclusion

This study assessed temperature-dependent effects (37 against 32 °C) of various *Bifidobacterium* probiotic species on QS gene expression in *Y. enterocolitica* during co-culturing. Results showed that temperature changes included distinct effects on gene expression and pathogenic and probiotic behaviors of the highlighted bacteria. Additionally, results demonstrated that temperature variations significantly altered gene expression patterns, which directly modulated pathogenic behaviors of *Y. enterocolitica* and probiotic effects of *Bifidobacterium* strains. At 32 °C, *Bifidobacterium* sp. produced inhibitory compounds that suppressed proliferation of *Y. enterocolitica* and downregulated QS-associated genes. Pathogenic activities of *Y. enterocolitica* were significantly terminated at this temperature, with decreased expression of QS genes. This suggested that at 32 °C, *Y. enterocolitica* could not fully activate its virulence pathways, weakening its ability to escape immune defenses and infect the host. In contrast, no significant differences were observed between the controls and the treated samples at 37 °C. This study highlights the critical roles of temperature in modulating bacterial interactions and potentially their pathogenic characteristics. At 32 °C, *Bifidobacterium* sp. effectively suppressed QS gene expression in *Y. enterocolitica*. At 37 °C, QS gene levels were largely unchanged in all cultures, similar to those in control samples. These findings have provided valuable highlights for developing probiotic-based strategies to prevent and/or help treat infections caused by *Y. enterocolitica* and other pathogens. However, further studies seem necessary.

5. Acknowledgements

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6. Declaration of competing interest

The authors report no conflict of interest.

7. Authors' Contributions

E.Y., Methodology, formal analysis, investigation, data curation and writing–original draft. M.K. and M.S.,

Conceptualization, methodology, investigation, data curation, writing–review and editing, supervision, project administration and funding acquisition. A.M., S.E. and E.G., Supervision, methodology, writing–review and editing and project administration.

8. Using Artificial Intelligent Chatbots

No AI chatbots or tools were used in this research in data analysis, scientific content generation or interpretation.

9. Ethical Consideration

This study did not involve human/animal subjects; thus no ethical approval was required.

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بررسی وابستگی دمایی بیان ژن های درک حد نصاب (*Yen I* و *Yen R*) در *Yersinia Enterocolitica* بوسیله گونه‌های مختلف پروبیوتیک *Bifidobacterium*

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چکیده

سابقه و هدف: به فرایند هماهنگی و ارتباط بین سلول‌ها، بوسیله ملکول‌های داخلی قابل انتشار که منجر به تنظیم بیان ژن می‌شود درک حد نصاب گویند، درک حد نصاب بر روی مواردی مانند بیماری‌زایی، چسبندگی، تحرک، تولید بیوفیلم و تجمع سلولی در پاتوژن‌ها موثر است لذا می توان با کنترل این سیگنال‌ها این عوامل را تحت تاثیر قرارداد.

مواد و روش ها: در این تحقیق اثر سه باکتری *B. lactis* ، *B.bifidum* و *B. longum* به صورت زنده بر میزان بیان ژن های سیستم درک حد نصاب در *Y. enterocolitica* در دماهای ۳۷ و ۳۲ درجه سانتی گراد مورد بررسی قرار گرفت. ابتدا باکتری ها تهیه و فعال سازی شد، سپس به صورت همزمان با *Y. enterocolitica* کشت داده شد، استخراج RNA انجام شد، میزان بیان ژن با استفاده از Real-time PCR بررسی شد

یافته‌ها و نتیجه‌گیری: نتایج این تحقیق نشان داد که در دماهای ۳۲ و ۳۷ درجه سانتی‌گراد، تفاوت‌های قابل توجهی در بیان ژن‌ها وجود دارد. کشت همزمان بیفیدوباکتریوم‌ها با *Y. enterocolitica* در دمای ۳۲ درجه سانتی گراد، نشان داد که مقدار بیان ژن های درک حد نصاب در تیمارها با نمونه کنترل ، دارای اختلاف معنی داری است و بیان ژن‌های سنجش حد نصاب روند کاهشی را نشان دادند. در این بین *B. longum* بیشترین اثر در کاهش بیان ژن با ۶۴ درصد را داشت. از طرفی در دمای ۳۷ درجه سانتی گراد، میزان بیان ژن‌های سنجش حد نصاب *Y. enterocolitica* در تیمارها نسبت به نمونه کنترل اختلاف معنی داری نداشت و تقریبا میزان بیان این ژن‌ها مانند مقدار بیان در نمونه کنترل بود. نتایج این تحقیق نشان داد نوع ارتباط بین باکتری‌های پروبیوتیک و پاتوژن‌ها در شرایط مختلف دمایی متفاوت است و رابطه‌ای وابسته به دما می باشد.

واژگان کلیدی: *بیفیدوباکتریوم*، بیان ژن، تنظیم ژن، سنجش حد نصاب، *یرسینیا انتروکولیتیکا*