

## Technological profile and antimicrobial potential of bacteria isolated from the gut of worker *Macrotermes subhyalinus* (Isoptera: Termitidae)

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### Abstract

Lactic acid bacteria (LAB) constitute a group of microorganisms of considerable interest in food biotechnology because of their technological properties and their ability to produce a wide range of antimicrobial metabolites. The present study aimed to evaluate the technological profile and antimicrobial potential of LAB isolated from the gut of worker *Macrotermes subhyalinus* collected in the Lamto region (Toumodi, Côte d'Ivoire). Four strains identified by 16S rRNA gene sequencing were selected: *Pediococcus acidilactici* KF806466.1, *Pediococcus pentosaceus* KF806470.1, *Lactobacillus brevis* KF806467.1, and *Lactobacillus plantarum* KF806469.1. Their technological properties were assessed by evaluating growth under different pH values, temperatures, and NaCl concentrations, as well as their production of organic acids, acidification capacity, and bacteriocin-producing ability. Antimicrobial activity was determined using the agar well diffusion method against *Bacillus subtilis* ATCC 6633, *Staphylococcus aureus* ATCC 25913, and *Pseudomonas aeruginosa* ATCC 27853. The results showed that all four strains exhibited optimal growth at pH 6.5 and 37 °C and displayed moderate tolerance to NaCl. Chromatographic analyses revealed a diverse production of organic acids, with lactic acid being the predominant metabolite. The *Pediococcus* strains exhibited the highest acidification capacity and produced substantial amounts of antimicrobial substances. The inhibition zone diameters demonstrated strong antibacterial activity, particularly for *P. pentosaceus* and *L. brevis*. These findings suggest that LAB isolated from the gut of *M. subhyalinus* represents a promising source of biotechnologically valuable strains that could be exploited as protective cultures and biopreservative agents in food systems.

**Keywords:** *Macrotermes subhyalinus*; Lactic acid bacteria; Technological properties; Organic acids; Bacteriocins; Antimicrobial activity; Biopreservation.

### 1. Introduction

Lactic acid bacteria (LAB) constitute a heterogeneous group of Gram-positive, non-spore-forming, generally catalase-negative microorganisms characterized by the production of lactic acid as the principal product of carbohydrate metabolism [1]. Owing to their fermentative properties and their ability to synthesize a wide range of bioactive metabolites, LAB plays a pivotal role in food fermentation processes and the natural preservation of foods [2]. These microorganisms have also attracted increasing interest in human health, the food industry, and biotechnology because of their Generally Recognized As Safe (GRAS) status and their numerous functional properties [3].

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Beyond conventional food environments, LAB are widely distributed in various natural ecosystems, including soils, plants, fermented products, and the gastrointestinal tract of animals and insects [4]. The insect gut constitutes a complex microenvironment in which symbiotic interactions occur between the host and its associated microorganisms. These microbial communities play essential roles in lignocellulose degradation, nutrition, defense against pathogens, and the maintenance of intestinal homeostasis [5].

Termites are recognized as remarkable biological models because of their exceptional ability to efficiently degrade lignocellulosic materials through the metabolic activities of microorganisms inhabiting their digestive tract [6]. In higher termites belonging to the family *Termitidae*, gut-associated bacteria actively participate in cellulose digestion, nitrogen fixation, and the synthesis of antimicrobial compounds that may protect the colony against undesirable microorganisms [7]. Among these termites, *Macrotermes subhyalinus* is a widespread species in the African savannas and maintains a mutualistic association with fungi of the genus *Termitomyces*, conferring remarkable diversity and metabolic potential to its gut microbiota [8].

In recent years, several studies have reported the occurrence of LAB belonging to the genera *Lactobacillus*, *Pediococcus*, *Enterococcus*, and *Weissella* in the digestive tract of insects, suggesting their involvement in host defense mechanisms and the production of metabolites of biotechnological interest [9]. Antimicrobial substances produced by these bacteria, including organic acids, hydrogen peroxide, and bacteriocins, can inhibit the growth of numerous spoilage bacteria and clinically relevant pathogens such as *Staphylococcus aureus*, *Bacillus subtilis*, and *Pseudomonas aeruginosa* [10, 11].

Furthermore, the technological characteristics of LAB, such as tolerance to variations in pH, elevated temperatures, and saline conditions, constitute essential criteria for their use as starter cultures or protective cultures in food fermentation processes [12]. Likewise, their ability to rapidly acidify growth media and produce a variety of organic acids contributes significantly to improving the microbiological safety and sensory quality of fermented foods [13].

Despite the ecological and economic importance of *Macrotermes subhyalinus*, limited attention has been devoted to the characterization of LAB associated with its digestive tract, particularly in West Africa. Exploring this ecological niche may facilitate the discovery of novel strains exhibiting valuable technological and antimicrobial properties for food and biotechnological applications.

In this context, the present study was undertaken to evaluate the technological profile and antimicrobial potential of lactic acid bacteria isolated from the gut of worker *Macrotermes subhyalinus* collected in the Lamto region of Côte d'Ivoire. Specifically, the study aimed to characterize their ability to grow under different physicochemical conditions, their capacity to produce organic acids and antimicrobial substances, and their inhibitory activity against selected bacterial pathogens of public health importance.

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## 2. Material and methods

### 2.1. Bacterial strains

The bacterial strains used in this study were isolated from the gut of worker *Macrotermes subhyalinus* collected in the Lamto region (Toumodi, Côte d'Ivoire). A total of four previously isolated and identified bacterial strains were selected for the analyses. Phenotypic and molecular identification revealed the following species: *Pediococcus acidilactici*, *Pediococcus pentosaceus*, *Lactobacillus brevis*, and *Lactobacillus plantarum*. The strains were preserved in de Man, Rogosa and Sharpe (MRS) broth supplemented with 20% (v/v) glycerol and stored at  $-80^{\circ}\text{C}$  until use. Before each experiment, the strains were reactivated by two successive subcultures in the appropriate growth medium and incubated under their optimal growth conditions.

### 2.2. Evaluation of the technological profile

#### 2.2.1. Growth at different pH values

The growth capacity of the bacterial strains under different pH conditions was evaluated in MRS broth, the initial pH of which was adjusted to 3.0, 6.5, and 9.0 using 1 N HCl or 1 N NaOH solutions. Each medium was inoculated with a standardized bacterial suspension and incubated under optimal temperature conditions for 24–48 h. Bacterial growth was assessed by measuring the optical density at 600 nm ( $\text{OD}_{600}$ ). The results were used to evaluate the tolerance and growth ability of each species under acidic, neutral, and alkaline conditions.

### 2.2.2. Growth at different temperatures

The growth capacity of the bacterial strains at different temperatures was evaluated in liquid MRS broth. The media were inoculated with standardized bacterial suspensions of the previously identified strains and incubated at 10, 30, 37, 45, and 51 °C for 24–48 h. Following incubation, bacterial growth was determined by measuring the optical density at 600 nm (OD<sub>600</sub>). This approach enabled the assessment of the isolates' ability to grow at low, moderate, and high temperatures, as well as the determination of their growth range and optimum growth temperature.

### 2.2.3. Tolerance to different NaCl concentrations

The sodium chloride (NaCl) tolerance of the bacterial strains isolated from worker *Macrotermes subhyalinus* was evaluated in MRS broth supplemented with different NaCl concentrations (0.5%, 5%, and 10%, w/v). Each medium was inoculated with a standardized bacterial suspension and incubated under optimal temperature conditions for 24–48 h. After incubation, bacterial growth was determined by measuring the optical density at 600 nm (OD<sub>600</sub>). The results were used to assess the ability of the different species to grow under increasing salt concentrations and to determine their degree of halotolerance.

### 2.2.4. Organic acid production

#### Sample preparation

The previously isolated and identified fermentative bacterial strains were purified and cultured in 10 mL of sterile sweet *tchapalo* wort (a traditional fermented sorghum beverage), the pH of which had been adjusted to 7.0 using 5 N KOH. A standardized inoculum was prepared by suspending bacterial colonies in 1 mL of sterile distilled water. Subsequently, 10% (v/v) of each inoculum was transferred into the *tchapalo* culture medium. After incubation at 30 °C for 24 h, the cultures were centrifuged at 4,000 rpm for 30 min, and the supernatants were filtered through 0.45- or 0.20-µm Millipore membrane filters (Sartorius AG, Göttingen, Germany) using sterile syringe filters (Sartorius). The resulting filtrates were stored at –20 °C until analysis. A non-inoculated sample was used as the control.

#### Determination of organic acids by HPLC

Chromatographic separation of organic acids was performed using an ORH-801 ion-exclusion column (300 mm × 6.5 mm; Interchrom, France) maintained at 35 °C with a MetaTherm™ column oven (Interchrom, France). The mobile phase consisted of 0.004 N sulfuric acid delivered at a flow rate of 0.8 mL min<sup>–1</sup>, and detection was carried out at 210 nm. A volume of 20 µL of each centrifuged and filtered sample was injected into the HPLC system. All analyses were performed in triplicate.

Organic acid standards were prepared in distilled water at concentrations ranging from 0.005 to 0.40 g L<sup>–1</sup>. The standards were filtered and injected individually. Organic acids were identified and quantified by comparing the retention times and peak areas of the standards with those obtained from the samples. Their concentrations were calculated from the mean peak areas of the reference solutions and the corresponding sample peaks and were expressed as g L<sup>–1</sup> [14].

### 2.2.5. Acidification capacity

The acidification capacity of the lactic acid bacterial strains was evaluated according to the method described by [15] by monitoring changes in the pH of the culture medium after incubation. Sterile MRS broth, previously adjusted to pH 7.0 using 5 N KOH, was inoculated with a single colony obtained from freshly purified cultures of each identified lactic acid bacterial strain.

The cultures were incubated at 30 °C, and acidification was monitored after 24 and 48 h to assess the ability of each strain to produce organic acids. Titratable acidity (%) was determined using 10 mL of culture, 0.1 N sodium hydroxide, and 1–3 drops of a 1% methanolic phenolphthalein solution as the indicator.

According to [16], the acidification parameters were calculated using the following equations :

$$\Delta\text{pH} = \text{pH (48 h)} - \text{initial pH}$$

$$\Delta\text{TA} = \text{titratable acidity (48 h)} - \text{initial titratable acidity}$$

### 2.2.6. Production of bacteriocins and other antimicrobial substances

The ability of the bacterial strains to produce bacteriocins or other antimicrobial compounds was evaluated using cell-free culture supernatants. The strains were cultivated in MRS broth and incubated under optimal growth conditions for 24–48 h. The cultures were subsequently centrifuged at 4,000 rpm for 15 min, and the cell-free supernatants were collected.

To eliminate the inhibitory effect of organic acids, the pH of each supernatant was adjusted to 6.5–7.0 using 0.1 N NaOH. In addition, hydrogen peroxide present in the culture supernatants was eliminated by treatment with catalase at 30 °C prior to antimicrobial testing. The residual antimicrobial activity, mainly attributed to bacteriocins or bacteriocin-like substances, was evaluated using the agar well diffusion assay against reference bacterial strains.

Briefly, 0.2 mL of each indicator strain culture was dispensed into sterile Petri dishes, followed by the addition of 20 mL of nutrient agar maintained at 45 °C. After solidification, three to four wells (6 mm in diameter) were punched into each agar plate. Subsequently, 100 µL of the neutralized and catalase-treated cell-free supernatant, obtained after centrifugation at 4,000 rpm for 15 min, was dispensed into each well. All experiments were performed in triplicate. Following incubation, the diameters of the inhibition zones were measured and expressed in millimeters (mm).

## 2.3. Evaluation of antimicrobial potential

### 2.3.1. Indicator strains

The antimicrobial activity of the bacterial strains isolated from the gut of worker *Macrotermes subhyalinus* was evaluated against several indicator microorganisms selected because of their relevance to public health and food microbiology. The indicator strains included the Gram-positive Bacteria *Staphylococcus aureus* and *Bacillus subtilis*, as well as the Gram-negative bacterium *Pseudomonas aeruginosa*.

The reference strains were cultured in Brain Heart Infusion (BHI) broth at 37 °C for 18–20 h. Subsequently, each strain was streaked onto nutrient agar and incubated at 37 °C for 24 h. The purity of the cultures was confirmed by Gram staining. Thereafter, selective culture media were used to verify specific phenotypic characteristics of each bacterial species. *Staphylococcus aureus* was confirmed on Chapman agar based on its ability to ferment mannitol, producing yellow colonies. *Bacillus subtilis* was isolated on Mossel agar, whereas *Pseudomonas aeruginosa* was isolated on Cetrimide agar.

After purification, the reference strains were maintained either on nutrient agar slants at room temperature or in nutrient broth supplemented with 20% (v/v) glycerol and stored at –80 °C until use. These pure cultures were subsequently used for the antimicrobial inhibition assays.

These indicator microorganisms were selected to determine the antimicrobial spectrum of the isolated lactic acid bacteria and to evaluate their potential application as bioprotective cultures or as producers of antimicrobial compounds of biotechnological interest. The reference strains used in this study are listed in Table 1.

**Table 1** Indicator strains used in antibacterial tests

| Bacterial species             | References |
|-------------------------------|------------|
| Gram-positive                 |            |
| <i>Staphylococcus aureus</i>  | ATCC 25913 |
| <i>Bacillus subtilis</i>      | ATCC 6633  |
| Gram-negative                 |            |
| <i>Pseudomonas aeruginosa</i> | ATCC 27853 |

ATCC: American Type Culture Collection

### 2.3.2. Antimicrobial activity assay

The antimicrobial activity of the isolates was evaluated using the agar well diffusion method described by [17]. The reference strains were first cultured in Brain Heart Infusion (BHI) broth at 30 °C. Subsequently, 0.2 mL of each indicator culture was transferred into sterile Petri dishes, followed by the addition of 20 mL of nutrient agar maintained in a

molten state at 45 °C. After solidification, wells measuring 6 mm in diameter were aseptically punched into the agar using a sterile cork borer without penetrating the bottom of the plates.

A volume of 100 µL of the previously prepared lactic acid bacterial suspension was then dispensed into each well. Before incubation at 37 °C for 18–24 h, the plates were pre-incubated at 5 °C for 4 h to facilitate the diffusion of antimicrobial substances into the agar medium. Inhibition zones with diameters  $\geq 8$  mm were considered indicative of positive antimicrobial activity. Antimicrobial activity was expressed as the diameter of the inhibition zone (mm).

### 2.3.3. 2.3.3. Measurement of inhibition zone diameters

The diameters of the inhibition zones were measured in millimeters using a graduated ruler. When the inhibition halos were not perfectly circular, two perpendicular diameters were measured, and their mean value was calculated. The results were expressed as the mean  $\pm$  standard deviation of three independent experiments.

## 2.4. Statistical analysis

The data obtained for bacterial growth under different pH values, temperatures, and NaCl concentrations, as well as for organic acid production, were subjected to analysis of variance (ANOVA) using Statistica software (version 7.1). When significant differences were detected among the evaluated parameters, mean values were separated using the Newman–Keuls multiple comparison test. Statistical significance was established at  $P < 0.05$ . The software was also used to calculate the mean values and standard deviations of all analyzed parameters, including bacterial growth under different pH and temperature conditions.

## 3. Results

### 3.1. Characteristics of the bacterial strains studied

Table 2 summarizes the characteristics of the bacterial strains selected for this study. Molecular analyses based on 16S rRNA gene sequencing enabled the identification of the isolates with high sequence similarity percentages ( $\geq 99\%$ ), indicating a close phylogenetic relationship with reference species deposited in GenBank. Among the isolates, strains S4 and S5 were identified as *Pediococcus acidilactici* and *Pediococcus pentosaceus*, with accession numbers KF806466 and KF806470, respectively. Strains S2 and S39 were assigned to the genus *Lactobacillus* and identified as *Lactobacillus brevis* (KF806467) and *Lactobacillus plantarum* (KF806469), respectively. These species were selected for the evaluation of their technological properties and antimicrobial potential.

**Table 2** Characteristics of the lactic acid bacteria strains used in this study

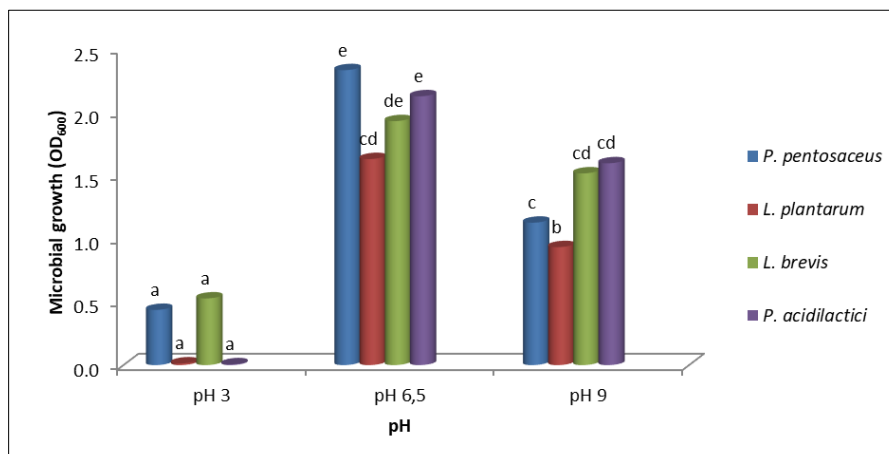
| Strain code | Species identified              | NCBI GenBank accession number | Origin of the isolation of the strains                          |
|-------------|---------------------------------|-------------------------------|-----------------------------------------------------------------|
| S4          | <i>Pediococcus acidilactici</i> | KF806466.1                    | Digestive tract of the worker of <i>Macrotermes subhyalinus</i> |
| S5          | <i>Pediococcus pentosaceus</i>  | KF806470.1                    |                                                                 |
| S2          | <i>Lactobacillus brevis</i>     | KF806467.1                    |                                                                 |
| S39         | <i>Lactobacillus plantarum</i>  | KF806469.1                    |                                                                 |

### 3.2. Technological profile of the bacterial strains

#### 3.2.1. Growth at different pH values

The growth of the four lactic acid bacteria was significantly affected by the pH of the culture medium ( $p < 0.05$ ). The highest optical density (OD) values were recorded at pH 6.5, with *Pediococcus pentosaceus* exhibiting the maximum growth (OD = 2.4). At pH 3.0, all strains showed poor growth, reflecting the inhibitory effect of highly acidic conditions, and no significant differences were observed among the strains at this pH. At pH 9.0, bacterial growth decreased; however, *Lactobacillus brevis* and *Pediococcus acidilactici* retained relatively high growth capacities. These findings

indicate that the strains are well adapted to variations in environmental pH. The significant differences observed ( $p < 0.05$ ) further demonstrate that pH 6.5 represents the optimal condition for bacterial growth.

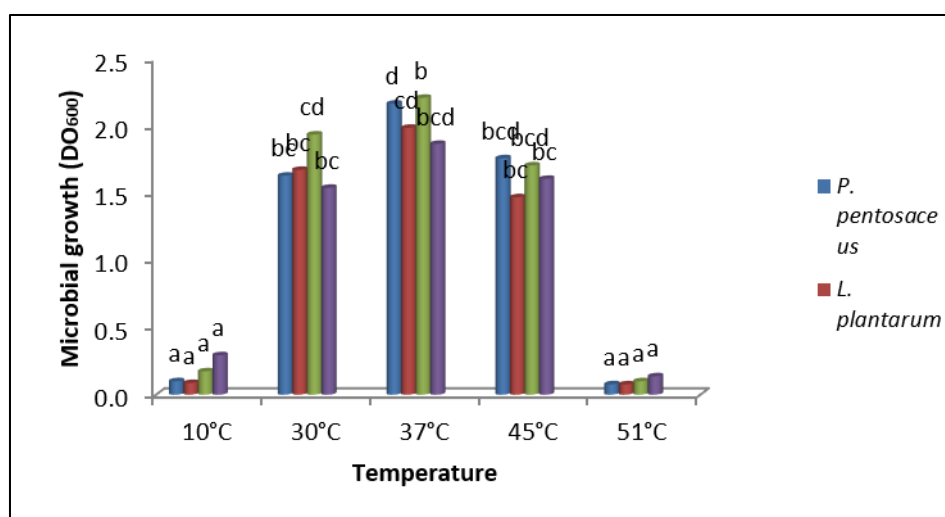


**Figure 1** Influence of pH on the growth of lactic acid bacteria species isolated from *Macrotermes subhyalinus* workers

### 3.2.2. Growth at different temperatures

Figure 2 illustrates the effect of temperature (10, 30, 37, 45, and 51 °C) on the growth of four lactic acid bacterial species (*Pediococcus pentosaceus*, *Lactiplantibacillus plantarum*, *Lactobacillus brevis*, and *Pediococcus acidilactici*) isolated from the gut of *Macrotermes subhyalinus* workers.

Temperature significantly influenced the growth of the lactic acid bacteria isolated from *Macrotermes subhyalinus* workers ( $p < 0.05$ ). Limited growth was observed at 10 and 51 °C, with optical density values below 0.4 and 0.2, respectively. The highest growth was recorded at 37 °C, where *Lactobacillus brevis* and *Pediococcus pentosaceus* exhibited the highest optical density values (2.3 and 2.2, respectively). At 45 °C, all lactic acid bacterial species maintained relatively high growth capacities, indicating a certain degree of thermotolerance. Overall, these results demonstrate that the studied strains are predominantly mesophilic, with an optimal growth temperature of approximately 37 °C.

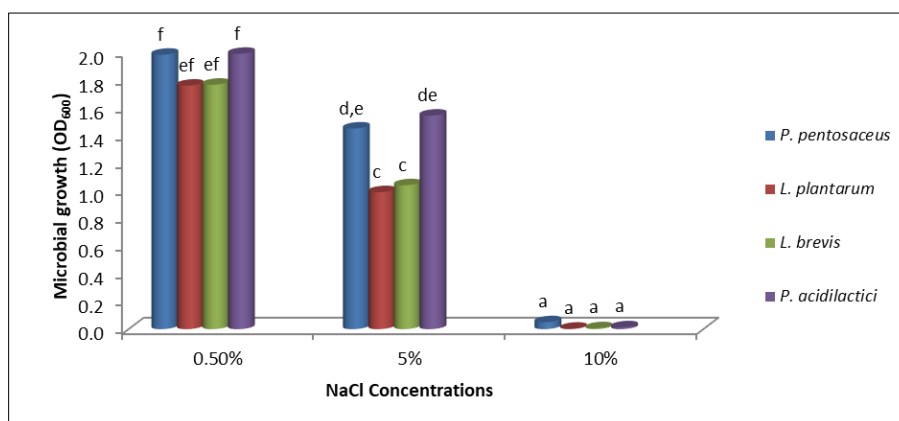


**Figure 2** Influence of temperature on the growth of lactic acid bacteria species isolated from *Macrotermes subhyalinus* workers.

### 3.2.3. NaCl tolerance

Figure 3 shows the effect of different NaCl concentrations (0.5%, 5%, and 10%) on the growth of four lactic acid bacterial species (*Pediococcus pentosaceus*, *Lactiplantibacillus plantarum*, *Lactobacillus brevis*, and *Pediococcus acidilactici*) isolated from the gut of *Macrotermes subhyalinus* workers. NaCl concentration significantly affected the growth of the

lactic acid bacteria ( $p < 0.05$ ). The highest growth was observed at 0.5% NaCl, with optical density (OD) values ranging from 1.8 to 2.0. A significant reduction in growth occurred at 5% NaCl, although *Pediococcus acidilactici* and *Pediococcus pentosaceus* exhibited the highest OD values (1.6 and 1.5, respectively). At 10% NaCl, the growth of all four strains was almost completely inhibited ( $OD < 0.2$ ). These results indicate that the studied strains are moderately halotolerant and that their growth is markedly affected by increasing osmotic pressure.

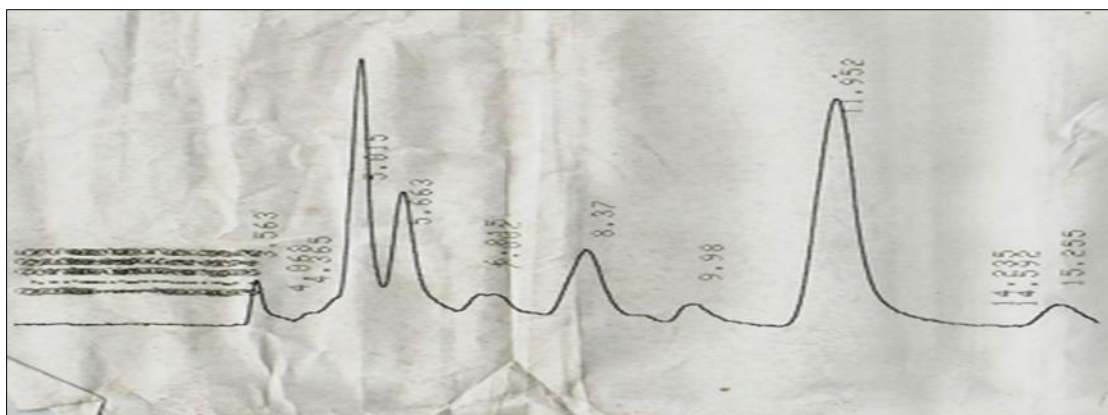


**Figure 3** Influence of NaCl concentrations on the growth of lactic acid bacteria species isolated from *Macrotermes subhyalinus* workers

#### 3.2.4. Organic acid production

Table 3 presents the concentrations of the major organic acids produced by the four lactic acid bacterial species isolated from the gut of *Macrotermes subhyalinus* workers. The results revealed significant differences ( $p < 0.05$ ) in the production of the various organic acids among the bacterial species, reflecting differences in their metabolic pathways and fermentative capacities.

The lactic acid bacterial species produced variable amounts of organic acids, with significant interspecies differences ( $p < 0.05$ ). Lactic acid was the predominant metabolite produced, particularly by *Lactobacillus brevis* ( $5.20 \pm 1.94$  g/L) and *Pediococcus pentosaceus* ( $4.00 \pm 0.42$  g/L). *L. brevis* also exhibited the highest production of acetic acid ( $2.07 \pm 3.07$  g/L), citric acid ( $5.77 \pm 0.39$  g/L), and ascorbic acid ( $2.25 \pm 0.39$  g/L). The diversity of the organic acids produced highlights the substantial metabolic activity of these strains and may contribute to their acidification capacity and antibacterial activity.



**Figure 4** HPLC chromatogram of organic acids produced by *Pediococcus pentosaceus* S5 isolated from the gut of *Macrotermes subhyalinus* workers.

The values shown on the chromatogram correspond to the retention times of the detected compounds: tannic acid (3.56 min), oxalic acid (4.36 min), citric acid (5.01 min), tartaric acid (5.60 min), lactic acid (6.81 min), propionic acid (8.37 min), acetic acid (11.95 min), and fumaric acid (15.25 min)

**Table 3** Acides organiques produits par les espèces de bactéries lactiques isolées de l'ouvrier de *M. subhyalinus*

| Organics acids (g/L) | Identified species of lactic acid bacteria |                                           |                                        |                                           |
|----------------------|--------------------------------------------|-------------------------------------------|----------------------------------------|-------------------------------------------|
|                      | <i>Pediococcus acidilactici</i> KF806466.1 | <i>Pediococcus pentosaceus</i> KF806470.1 | <i>Lactobacillus brevis</i> KF806467.1 | <i>Lactobacillus plantarum</i> KF806469.1 |
| Acetic acid          | 0.27 ± 0.2 <sup>b</sup>                    | 0.016 ± 0.005 <sup>c</sup>                | 2.07 ± 3.07 <sup>a</sup>               | 0.1 ± 0.025 <sup>b</sup>                  |
| Ascorbic acid        | 0.85 ± 0.65 <sup>b</sup>                   | 0.44 ± 0.06 <sup>c</sup>                  | 2.25 ± 0.39 <sup>a</sup>               | 0.01 ± 0.005 <sup>d</sup>                 |
| Citric acid          | 2.65 ± 0.65 <sup>c</sup>                   | 0.14 ± 0.03 <sup>d</sup>                  | 5.77 ± 0.39 <sup>a</sup>               | 1.14 ± 0.11 <sup>b</sup>                  |
| Fumaric acid         | 0.17 ± 0.06 <sup>b</sup>                   | 0.083 ± 0.025 <sup>c</sup>                | 0.33 ± 0.17 <sup>a</sup>               | 0.016 ± 0.005 <sup>d</sup>                |
| Lactic acid          | 0.9 ± 0.13 <sup>c</sup>                    | 4 ± 0.42 <sup>a</sup>                     | 5.2 ± 1.94 <sup>a</sup>                | 3.1 ± 0.56 <sup>b</sup>                   |
| Oxalic acid          | 0.71 ± 0.42 <sup>a</sup>                   | 0.88 ± 0.11 <sup>a</sup>                  | 0.95 ± 0.38 <sup>a</sup>               | 0.41 ± 0.27 <sup>b</sup>                  |
| Tannic Acid          | 1.37 ± 0.43 <sup>a</sup>                   | 0.64 ± 0.11 <sup>c</sup>                  | 1.7 ± 0.43 <sup>a</sup>                | 0.95 ± 0.12 <sup>b</sup>                  |
| Tartric Acid         | 0.88 ± 0.31 <sup>c</sup>                   | 0.2 ± 0.05 <sup>d</sup>                   | 0.5 ± 0.29 <sup>c</sup>                | 1 ± 0.14 <sup>b</sup>                     |

Within the same row, values followed by the same letter are not statistically different ( $P > 0.05$ ).

### 3.2.5. Acidifying capacity

Table 4 presents the acidifying capacity of the four lactic acid bacterial species isolated from the gut of *Macrotermes subhyalinus* workers, as evaluated by the decrease in pH ( $\Delta\text{pH}$ ) and the increase in titratable acidity ( $\Delta\text{TA}$ ). All four species exhibited a strong acidifying capacity, with pH reductions ranging from  $2.10 \pm 0.21$  to  $2.21 \pm 0.03$  and titratable acidity values ranging from  $1.18 \pm 0.31\%$  to  $1.35 \pm 0.55\%$ . The *Pediococcus* species, particularly *Pediococcus pentosaceus* KF806470.1 ( $\Delta\text{TA} = 1.35 \pm 0.55\%$ ) and *Pediococcus acidilactici* KF806466.1 ( $\Delta\text{TA} = 1.31 \pm 0.28\%$ ), displayed significantly greater acidification capacities ( $p < 0.05$ ) than *Lactobacillus brevis* and *Lactobacillus plantarum*. These findings highlight the technological potential of these strains for fermentation processes and their ability to contribute to food biopreservation through the production of organic acids. Overall, the results demonstrate that all the strains possess a high capacity for organic acid production, with particularly strong performance observed in the *Pediococcus* species.

**Table 4** Changes in acidifying capacity ( $\Delta\text{pH}$  and  $\Delta\text{TA}$ ) of lactic acid bacterial species isolated from the gut of *Macrotermes subhyalinus* workers.

| Species of lactic acid bacteria            | Parameters        |                       |
|--------------------------------------------|-------------------|-----------------------|
|                                            | $\Delta\text{pH}$ | $\Delta\text{TA}(\%)$ |
| <i>Pediococcus acidilactici</i> KF806466.1 | 2.2±0.03b         | 1.31±0.28a            |
| <i>Pediococcus pentosaceus</i> KF806470.1  | 2.21±0.03a        | 1.35±0.55a            |
| <i>Lactobacillus brevis</i> KF806467.1     | 2.21±0.03a        | 1.19±0.24b            |
| <i>Lactobacillus plantarum</i> KF806469.1  | 2.1±0.21a         | 1.18±0.31b            |

**$\Delta\text{pH}$**  : Change in pH;  **$\Delta\text{TA}$**  : Change in titratable acidity (%). Values are expressed as the mean of three independent replicates. Within the same column, values followed by the same letter are not significantly different ( $p > 0.05$ ).

### 3.2.6. Bacteriocin production

The putative bacteriocins produced by the lactic acid bacteria isolated from the gut of *Macrotermes subhyalinus* workers exhibited variable antibacterial activity depending on both the producer strain and the indicator microorganism (Table 5). The inhibition zone diameters ranged from  $4.18 \pm 0.91$  to  $11.33 \pm 0.91$  mm. *Pediococcus acidilactici* KF806466.1 exhibited the broadest antibacterial spectrum, producing inhibition zones of  $9.85 \pm 1.21$  mm against *Bacillus subtilis*,  $10.66 \pm 1.42$  mm against *Staphylococcus aureus*, and  $11.28 \pm 0.57$  mm against *Pseudomonas aeruginosa*. These findings suggest that *Pediococcus* species possess a high potential for bacteriocin production and could be exploited as protective cultures and biopreservative agents in food fermentation processes.

**Table 5** Antibacterial activity of putative bacteriocins produced by lactic acid bacterial species isolated from the gut of *Macrotermes subhyalinus* workers.

| Species of lactic acid bacteria            | Reference strains after 48 hours of culture |                                              |                                               |
|--------------------------------------------|---------------------------------------------|----------------------------------------------|-----------------------------------------------|
|                                            | <i>Bacillus subtilis</i><br>(ATCC 6633)     | <i>Staphylococcus aureus</i><br>(ATCC 25913) | <i>Pseudomonas aeruginosa</i><br>(ATCC 27853) |
| <i>Pediococcus acidilactici</i> KF806466.1 | 9.85 ± 1.21 <sup>b</sup>                    | 10.66 ± 1.42 <sup>a</sup>                    | 11.28 ± 0.57 <sup>a</sup>                     |
| <i>Pediococcus pentosaceus</i> KF806470.1  | 8.81 ± 0.36 <sup>b</sup>                    | 11.33 ± 0.91 <sup>a</sup>                    | 8.12 ± 0.9 <sup>b</sup>                       |
| <i>Lactobacillus brevis</i> KF806467.1     | 10.5 ± 1.31 <sup>a</sup>                    | 7.42 ± 0.61 <sup>b</sup>                     | 6.7 ± 0.9 <sup>cd</sup>                       |
| <i>Lactobacillus plantarum</i> KF806469.1  | 6.66 ± 0.87 <sup>c</sup>                    | 11.32 ± 1.35 <sup>a</sup>                    | 4.18 ± 0.91 <sup>d</sup>                      |

D : inhibition zone diameter (mm). 0 < D < 5 mm : no antimicrobial activity ; 6 < D < 10 mm : moderate antimicrobial activity ; 11 < D < 21 mm : strong antimicrobial activity. Values are expressed as the mean of three independent replicates. Within the same column, values followed by the same lowercase letter are not significantly different ( $p > 0.05$ ) according to the Newman-Keuls multiple comparison test ( $n = 3$ ).

### 3.3. Antimicrobial activity of the strains

The lactic acid bacteria isolated from the gut of *Macrotermes subhyalinus* workers exhibited variable antibacterial activities against the reference strains tested after 48 h of incubation (Table 6). The inhibition zone diameters ranged from 6.16 ± 1.75 to 18.50 ± 4.82 mm. *Pediococcus pentosaceus* KF806470.1 and *Lactobacillus brevis* KF806467.1 exhibited the strongest antibacterial activity against *Bacillus subtilis*, with inhibition zones of 18.50 ± 4.82 mm and 18.33 ± 3.05 mm, respectively. Similarly, *P. pentosaceus* showed strong inhibitory activity against *Staphylococcus aureus* (17.33 ± 2.51 mm) and *Pseudomonas aeruginosa* (14.33 ± 1.15 mm). These results demonstrate the considerable antimicrobial potential of the studied strains and support their prospective application in food biopreservation strategies.

**Table 6** Antibacterial activity of lactic acid bacterial species isolated from the gut of *Macrotermes subhyalinus* workers against reference strains, expressed as inhibition zone diameters (mm).

| Species of lactic acid bacteria            | Reference strains after 48 hours of culture |                                              |                                               |
|--------------------------------------------|---------------------------------------------|----------------------------------------------|-----------------------------------------------|
|                                            | <i>Bacillus subtilis</i><br>(ATCC 6633)     | <i>Staphylococcus aureus</i><br>(ATCC 25913) | <i>Pseudomonas aeruginosa</i><br>(ATCC 27853) |
| <i>Pediococcus acidilactici</i> KF806466.1 | 13.16 ± 5.5a                                | 11 ± 0.64c                                   | 11.83 ± 3.32b                                 |
| <i>Pediococcus pentosaceus</i> KF806470.1  | 18.5 ± 4.82b                                | 17.33 ± 2.51a                                | 14.33 ± 1.15a                                 |
| <i>Lactobacillus brevis</i> KF806467.1     | 18.33 ± 3.05b                               | 15.33 ± 6.65b                                | 12 ± 3b                                       |
| <i>Lactobacillus plantarum</i> KF806469.1  | 13.16 ± 2.36a                               | 11.33 ± 8.14c                                | 6.16 ± 1.75c                                  |

D : inhibition zone diameter (mm). 0 < D < 5 mm : no antimicrobial activity ; 6 < D < 10 mm : moderate antimicrobial activity ; 11 < D < 21 mm : strong antimicrobial activity. Values are expressed as the mean of three independent replicates. Within the same column, values followed by the same lowercase letter are not significantly different ( $p > 0.05$ ) according to the Newman-Keuls multiple comparison test ( $n = 3$ ).

## 4. Discussion

The results obtained in the present study demonstrate the occurrence of lactic acid bacteria with remarkable technological and antimicrobial properties in the gut of worker *Macrotermes subhyalinus*. These findings further support the role of the termite gut microbiota as a reservoir of microorganisms with considerable potential for food and biotechnological applications.

The four bacterial species exhibited optimal growth at pH 6.5, whereas a significant reduction in growth was observed under highly acidic (pH 3) and alkaline (pH 9) conditions. These findings are consistent with those reported by [12], who stated that lactic acid bacteria are generally neutrophilic to slightly acidophilic, with optimal growth occurring between pH 5.5 and 7.0. The low optical densities recorded at pH 3 may be attributed to acid stress, which disrupts the transmembrane proton gradient, causes partial protein denaturation, and reduces metabolic activity. According to [18], these effects result from the inhibitory action of high  $H^+$  ion concentrations on enzymatic functions and membrane permeability.

The ability of *Lactobacillus brevis* and *Pediococcus acidilactici* to maintain relatively high growth under alkaline conditions demonstrates their remarkable adaptation to basic environments and considerable physiological plasticity, characteristics that are highly desirable for probiotic cultures and starter cultures used in fermentation processes. This tolerance may also be associated with their capacity to regulate intracellular pH and preserve the integrity of their enzymatic systems. Similar observations have been reported for strains of *Lactobacillus plantarum* and *Pediococcus pentosaceus* isolated from traditional African fermented foods [19].

The strains investigated exhibited optimal growth at 37 °C, whereas only limited proliferation was observed at 10 °C and 51 °C. This observation is consistent with the physiological characteristics of most lactic acid bacteria, whose optimum growth temperature generally ranges between 30 and 40 °C. Moderate temperatures enhance enzymatic activity, membrane fluidity, and the efficiency of metabolic processes, thereby promoting increased cellular proliferation.

These findings confirm the mesophilic nature of the studied lactic acid bacteria, as previously reported by [1]. The reduction in growth observed at 45 °C indicates that the strains begin to experience thermal stress, which may result in partial protein denaturation and impairment of essential metabolic enzymes. Nevertheless, the relatively high optical densities maintained at this temperature indicate a certain degree of thermotolerance, a desirable characteristic for their application in fermentation processes requiring moderately elevated temperatures.

The particularly strong performance of *L. brevis* and *P. pentosaceus* within the temperature range of 30–45 °C suggests that these strains may be especially suitable for industrial applications requiring tolerance to temperature fluctuations, particularly in food fermentation processes and the production of antimicrobial compounds. These findings are in agreement with those of [2], who demonstrated that several species of the genera *Lactobacillus* and *Pediococcus* possess a broad temperature growth range, enabling their adaptation to diverse environmental conditions.

All strains exhibited satisfactory growth at low salt concentrations, whereas almost complete growth inhibition was observed at 10% NaCl, indicating that this concentration exceeds their osmotic adaptation capacity. These results suggest that the studied strains are moderately halotolerant. Similar findings were reported by [16], who showed that lactic acid bacteria isolated from fermented dairy products generally remain metabolically active at NaCl concentrations ranging from 6% to 8%.

The *Pediococcus* species exhibited the highest growth capacity under saline conditions, which may be attributed to their ability to maintain intracellular osmotic balance through the accumulation of compatible solutes. This characteristic represents a valuable advantage for their application in high-salt fermented foods. Indeed, previous studies have demonstrated that certain *Pediococcus* species can tolerate NaCl concentrations ranging from 5% to 6.5% owing to efficient osmotic regulation mechanisms and their ability to accumulate osmoprotective compounds [20, 21]. The ability of *P. acidilactici* and *P. pentosaceus* to sustain relatively high growth at 5% NaCl is therefore of considerable biotechnological interest. These strains could be exploited as starter cultures for moderately salted fermented foods or as protective cultures in biopreservation processes where salt tolerance is an important selection criterion.

The high lactic acid production observed in *Lactobacillus brevis* ( $5.2 \pm 1.94$  g/L) and *Pediococcus pentosaceus* ( $4.0 \pm 0.42$  g/L) is consistent with the metabolic characteristics of lactic acid bacteria. Lactic acid is the primary end product of carbohydrate fermentation and represents one of the principal mechanisms involved in food biopreservation. According to [22], lactic acid production lowers the pH of the surrounding environment, thereby inhibiting the growth of numerous spoilage and pathogenic microorganisms. These findings are also consistent with those reported by [2], who described lactic acid production as the predominant metabolic pathway of lactic acid bacteria.

The particularly high citric acid production observed in *L. brevis* ( $5.77 \pm 0.39$  g/L) may be attributed to the obligately heterofermentative nature of this species. In addition to lactic acid, heterofermentative bacteria produce acetic acid, ethanol, and carbon dioxide through the phosphoketolase pathway of pentose phosphate metabolism. [23] reported that *L. brevis* can produce a broad spectrum of organic metabolites that contribute both to food preservation and to the development of the sensory characteristics of fermented products.

The relatively high citric acid concentrations produced by *L. brevis* and *P. acidilactici* are of considerable technological interest. Citric acid functions as a natural acidulant and chelating agent. [21] demonstrated that the production of secondary organic acids enhances both the preservative properties and the sensory quality of fermented foods.

The absence of significant differences in oxalic acid production among *P. acidilactici*, *P. pentosaceus*, and *L. brevis* suggests that the metabolic pathways involved in its biosynthesis are relatively similar in these species. In contrast, the lower oxalic acid production observed in *L. plantarum* may reflect differences in carbon substrate metabolism.

Acidification capacity is a major technological criterion for selecting lactic acid bacteria intended for food fermentation processes. The substantial reductions in pH ( $\Delta\text{pH} \approx 2.1\text{--}2.2$ ) observed in this study demonstrate the high fermentative activity of the strains isolated from worker *Macrotermes subhyalinus*. This acidification is mainly attributable to the production of organic acids, particularly lactic acid, resulting from the metabolism of fermentable carbohydrates. According to [22], lactic acid bacteria can rapidly lower the pH of the culture medium through the production of large amounts of lactic acid, thereby contributing to food preservation and inhibiting the growth of undesirable microorganisms.

The high  $\Delta\text{TA}$  values recorded for *Pediococcus pentosaceus* and *Pediococcus acidilactici* indicate a greater capacity for organic acid production. This characteristic may be associated with higher glycolytic enzyme activity and a more efficient conversion of sugars into lactic acid. [21] reported that *Pediococcus* species generally exhibit strong acidifying capacity and are widely employed as starter cultures and biopreservative agents because of their ability to rapidly produce organic acids and bacteriocins.

The lower  $\Delta\text{TA}$  values observed for *Lactobacillus brevis* and *Lactobacillus plantarum* may be explained by their fermentative metabolism. *L. brevis* is an obligately heterofermentative bacterium that produces not only lactic acid but also acetic acid, ethanol, and  $\text{CO}_2$ , thereby reducing the proportion of lactic acid formed and consequently the measurable titratable acidity. [23] reported that heterofermentative lactic acid bacteria generally exhibit slower acidification rates and lower lactic acid production than homofermentative species.

Furthermore, the strong acidification exhibited by all four strains represents a major ecological and technological advantage. Lowering the pH below the optimal growth range of many pathogenic microorganisms contributes significantly to the microbiological safety of fermented foods. According to [24] and [25], the production of organic acids by lactic acid bacteria constitutes one of the principal mechanisms underlying the biopreservation of fermented foods by reducing pH and inhibiting the growth of spoilage and pathogenic microorganisms.

The ability of the strains isolated from *Macrotermes subhyalinus* to produce substantial amounts of organic acids also suggests their probiotic potential. Indeed, acidification of the surrounding environment promotes the competitive exclusion of undesirable microorganisms and contributes to maintaining the balance of the intestinal microbiota. [26] reported that a high acidification capacity is frequently associated with favorable technological and probiotic properties in lactic acid bacteria.

The results further demonstrated that the lactic acid bacteria isolated from worker *Macrotermes subhyalinus* produces antimicrobial substances capable of inhibiting both Gram-positive bacteria (*Bacillus subtilis* and *Staphylococcus aureus*) and the Gram-negative bacterium *Pseudomonas aeruginosa*. This antimicrobial activity is most likely associated with the production of putative bacteriocins, possibly acting synergistically with other antimicrobial metabolites such as organic acids, hydrogen peroxide, and antifungal compounds. According to [27] and [28], the antagonistic activity of lactic acid bacteria results from the production of a wide range of bioactive metabolites, including organic acids, bacteriocins, hydrogen peroxide, and diacetyl, which collectively contribute to the inhibition of undesirable microorganisms and the biopreservation of foods.

The pronounced antimicrobial activity exhibited by *Pediococcus acidilactici* is consistent with the characteristics of the genus *Pediococcus*, which is well known for producing pediocin-type bacteriocins, particularly Pediocin PA-1. This bacteriocin displays a broad antimicrobial spectrum and can inhibit numerous foodborne pathogens and spoilage microorganisms. [29] demonstrated that *P. acidilactici* produces thermostable bacteriocins active against a wide range of Gram-positive bacteria. Likewise, [11] highlighted the importance of these antimicrobial peptides in food biopreservation.

The marked inhibition observed against *Staphylococcus aureus* (10.66–11.33 mm) indicates a high susceptibility of this pathogen to the antimicrobial metabolites produced by the studied strains. Similar findings were reported by [30], who demonstrated the effectiveness of bacteriocins produced by lactic acid bacteria against several foodborne pathogens, including *S. aureus*.

The inhibition of *Pseudomonas aeruginosa* by *Pediococcus acidilactici* is particularly noteworthy because Gram-negative bacteria are generally more resistant to bacteriocins produced by lactic acid bacteria owing to the presence of an outer

membrane rich in lipopolysaccharides, which acts as an effective permeability barrier. According to [23], bacteriocins produced by lactic acid bacteria primarily target Gram-positive bacteria, whereas their activity against Gram-negative bacteria is generally limited or dependent on the combined action of several antimicrobial metabolites, particularly organic acids and other secondary antimicrobial compounds. The comparatively weak activity of *Lactobacillus plantarum* against *P. aeruginosa* ( $4.18 \pm 0.91$  mm), as well as that of *L. brevis* ( $6.70 \pm 0.90$  mm), may therefore be explained by a lower production of bacteriocins or by a narrower antimicrobial spectrum. Nevertheless, their inhibitory activity against *S. aureus* suggests that these species also possess promising biopreservative potential.

Overall, the results demonstrate that the lactic acid bacteria isolated from worker *Macrotermes subhyalinus* possess strong antagonistic activity against the reference bacterial strains tested. The inhibition zone diameters exceeding 11 mm for most of the isolates indicate a high level of antimicrobial activity according to the adopted interpretation criteria.

This inhibitory activity can be attributed to the production of several antimicrobial metabolites, including organic acids, bacteriocins, hydrogen peroxide, and other bioactive compounds synthesized by lactic acid bacteria.

The strong inhibitory activity of *Pediococcus pentosaceus* against *Bacillus subtilis* and *Staphylococcus aureus* is consistent with the well-established characteristics of the genus *Pediococcus*, which is widely recognized for producing pediocin-type bacteriocins. These antimicrobial peptides exhibit particularly potent activity against numerous Gram-positive bacteria. [29] reported that *P. pentosaceus* strains produce thermostable bacteriocins capable of effectively inhibiting several pathogenic and spoilage microorganisms.

The large inhibition zones produced by *Lactobacillus brevis* against *B. subtilis* (18.33 mm) and *S. aureus* (15.33 mm) may be attributed to its high production of organic acids, particularly lactic, acetic, and citric acids, as demonstrated in the present study. Organic acids exert their antimicrobial effects by lowering the environmental pH and disrupting the intracellular metabolism of susceptible bacteria. [23] reported that the synergistic interaction between organic acids and bacteriocins substantially enhances the antimicrobial activity of lactic acid bacteria.

The inhibition of *Pseudomonas aeruginosa* by *P. pentosaceus*, *P. acidilactici*, and *L. brevis* is particularly significant. Gram-negative bacteria are generally more resistant to antimicrobial substances produced by lactic acid bacteria because their outer membrane, rich in lipopolysaccharides, restricts the penetration of antimicrobial compounds. [30] suggested that the inhibitory activity of lactic acid bacteria against Gram-negative bacteria often results from the synergistic action of organic acids, bacteriocins, and other antimicrobial metabolites.

The relatively low inhibitory activity exhibited by *Lactobacillus plantarum* against *P. aeruginosa* (6.16 mm) suggests either a lower production of antimicrobial compounds active against Gram-negative bacteria or a narrower spectrum of activity of its bacteriocins. Nevertheless, the inhibition zone diameters exceeding 11 mm against Gram-positive bacteria confirm its promising potential as a biopreservative culture.

The strong antibacterial activities observed for *Pediococcus pentosaceus* and *Lactobacillus brevis* suggest that these strains could be exploited as protective cultures or as sources of natural antimicrobial compounds for food fermentation and biopreservation processes.

Overall, the technological properties, capacity for organic acid production, and pronounced antibacterial activity exhibited by the strains isolated from the gut of worker *Macrotermes subhyalinus* confirm the considerable biotechnological potential of this still largely unexplored ecological niche. These bacteria could be exploited as protective cultures or as natural sources of antimicrobial compounds for food biopreservation and the development of novel probiotic products.

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## 5. Conclusion

The present study highlighted the technological properties and antimicrobial potential of four lactic acid bacteria isolated from the gut of worker *Macrotermes subhyalinus*, namely *Pediococcus acidilactici* KF806466.1, *Pediococcus pentosaceus* KF806470.1, *Lactobacillus brevis* KF806467.1, and *Lactobacillus plantarum* KF806469.1.

The results demonstrated that these strains are able to grow under a wide range of physicochemical conditions, with optimal growth occurring at pH 6.5 and 37 °C. They also exhibited moderate tolerance to sodium chloride, a desirable characteristic for their potential application in various food fermentation processes.

Chromatographic analyses revealed substantial and diverse production of organic acids, with lactic acid being the predominant metabolite, reflecting their high metabolic activity. The *Pediococcus* strains exhibited the greatest acidification capacity and showed a remarkable ability to produce bacteriocin-like antimicrobial substances.

Furthermore, all the isolates displayed significant antibacterial activity against *Bacillus subtilis*, *Staphylococcus aureus*, and *Pseudomonas aeruginosa*, with particularly strong inhibitory effects observed for *Pediococcus pentosaceus* and *Lactobacillus brevis*. These characteristics underscore their considerable potential for applications in food biopreservation and food biotechnology.

Overall, the gut of *Macrotermes subhyalinus* represents a promising ecological niche harboring lactic acid bacterium with valuable technological and antimicrobial properties. Further studies focusing on the purification and molecular characterization of the bacteriocins produced, the assessment of their safety, and the evaluation of their probiotic potential are warranted to support their future exploitation in the food, pharmaceutical, and nutraceutical industries.

## Compliance with ethical standards

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### Disclosure of conflict of interest

The authors declare that they have no competing interests related to the content or the findings reported in this article.

### Statement of ethical approval

Ethical review and approval were not required for this study involving human participants. The paper has been sufficiently anonymized to maintain the patient's confidentiality.

### Author contributions

All authors contributed equally to producing this manuscript

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