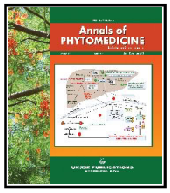
Annals of Phytomedicine 12(2): 120-130, 2023

DOI: http://dx.doi.org/10.54085/ap.2023.12.2.14

Annals of Phytomedicine: An International Journal
http://www.ukaazpublications.com/publications/index.php

Print ISSN : 2278-9839 Online ISSN : 2393-9885



Review Article : Open Access

Antimicrobial potential of lactic acid bacteria against food spoilage and foodborne pathogenic bacteria

Anupam Sharma, Vikrant, Priyanka and Wamik Azmi◆

Department of Biotechnology, Himachal Pradesh University, Shimla-171005, Himachal Pradesh, India

Article Info

Article history
Received 1 August 2023
Revised 16 September 2023
Accepted 17 September 2023
Published Online 30 December 2023

Keywords
Lactic acid bacteria
Bacteriocins
Antimicrobial metabolites
Foodborne pathogen

Abstract

Deterioration of food during storage is a major cause of concern for food industries especially, in tropical countries. Food is rich in nutrients and apposite for the growth and reproduction of pathogenic microorganisms. As per the UNEP Food Waste Index Report (2021), approximately 17% of the total global food available to consumers ended up in the trash barrels of households, restaurants, retailers and other food services and its major cause is microbial contamination. Microbial contamination can cause significant changes in the characteristics of food such as nutritional value, texture, smell and flavour. Some microbial agents produce toxins and chemicals that can cause serious damage to human health. Because of this, various physical and chemical methods are used by the food industry to produce food products that are free from contamination but these methods can also alter the sensorial and nutritional properties of food. Considering the interest of consumers towards the food that is nutritionally balanced, good in taste, and free from any chemical treatment, lactic acid bacteria (LAB) can play a great role as an antimicrobial alternative. Various fermented foods naturally contain LAB which are Gram-positive, cocci, or rod in shape and are known to restrict the growth of food spoilage and foodborne pathogens because of their antimicrobial activities. These antimicrobial activities are due to the production of several antimicrobial metabolites, particularly bacteriocins. By emphasizing the significance of LAB, this review offers a thorough overview of emerging approaches to the control of foodborne pathogens.

1. Introduction

Microbial contamination of food is a major challenge in food industries. Various factors such as temperature, pH, substrate base, origin, available water and atmosphere play an important role in microbial growth and also decide which microorganisms dominate and spoil food (Rolfe and Daryaei, 2020). Various microorganisms associated with food spoilage and foodborne diseases are bacteria such as *Bacillus cereus*, *Campylobacter jejuni, Escherichia coli, Shigella* spp., *Staphylococcus aureus,* viruses, *e.g.*, noroviruses, hepatitis A and fungi. These microorganisms spoil the same or different food products and spoiled food may lead to foodborne illness and big loss to food industries. Humans can suffer very serious health damage from consumption of contaminated food and in rare cases, this damage may be fatal (Barbosa *et al*., 2021). According to a World Health Organisation (WHO) report, over 200 diseases are caused by ingesting contaminated food. As per the One Health Zoonoses report released by the EU in 2021, there were 4,005 foodborne outbreaks in the EU-which is 29.8% more compared with 2020.

It takes numerous steps to get food from the farms to the dining table and it can be contaminated at any point of production, processing, distribution and preparation. Foodborne outbreaks most frequently occur in restaurants, cafeterias and canteens *via* cross-contamination, inadequate cooking, and improper storage during summers. It is known that bacteria are able to grow on food matrixes, along with food industry set-up and this growth may give rise to biofilm. Biofilm is an aggregate of bacterial cells in which, bacterial cells are stuck to each other or to a solid surface. Biofilms show structural heterogeneity, genetic diversity and community interaction and the major benefit they provide is increased resistance to detergents and antibiotics. During biofilm formation, the bacterial cells embed themselves in the self-produced matrix of extracellular polymeric substances (EPS), which is a polymeric jumble of eDNA, proteins and polysaccharides (Kanwar *et al*., 2019). It is also reported that *Salmonella* spp. are capable of forming biofilms on the utensils and food contact surfaces of food industries even at a low temperature of 3°C (Akinola *et al*., 2020). *Salmonella* spp. found to be more resistant to sanitizers (chlorine and iodine) than planktonic cells, so there is a need to develop methods to control microbial contamination (Joseph *et al*., 2001; Chatterjee and Abraham, 2018). There is a variety of preventive methods that are being used by different food industries such as the use of several chemicals as disinfectants or as food preservatives, heat treatment (thermal technique), and non-thermal technique (electrolyte oxidizing water, high-pressure processing, high-light intensity technique, ultrasonic technology). But sometimes, such methods or treatments adversely impact the sensorial and nutritional properties of the food. Consumer awareness about food safety and healthy food products has caused an increased interest in natural and effective antimicrobial alternatives. LAB and their

Corresponding author: Dr. Wamik Azmi
Department of Biotechnology, Himachal Pradesh University, Shimla-171005, Himachal Pradesh, India
E-mail: wamikazmi@rediffmail.com
Tel.: +91-9418311183

metabolites have great potential to inhibit the growth of food spoilage and foodborne bacteria and can be used as a potent antimicrobial alternative as well as a bio-preservative agent.

2. Food spoilage bacteria

Spoilage of food products is done by various microorganisms and chemicals, which consequently bring changes in the visual, texture, and smell of food and make it undesirable or unacceptable for human consumption (Soni *et al*., 2022). Most natural foods such as fruits, vegetables, meat, milk and breads generally have short shelf-life and get spoiled easily. In food industries, food can become susceptible to microbial spoilage due to the lack of proper refrigeration, storing raw and processed food together and compromised hygiene. Various microorganisms are able to spoil food but bacteria are the major cause of food spoilage. Sometimes bacteria are not harmful but the metabolites they produce after the breakdown of food nutrients, for example, acids and volatile compounds become the cause of foodborne illness (Tull,1997). In Table 1 various bacteria, the food stuffs they spoil and some spoilage products they produced after spoilage are listed.

Table1: Food products spoiled by bacteria and their spoilage products

Bacteria	Foodstuff/product	Spoilage product
Pseudomonas, Acinetobacter, Moraxella, E. coli, Staphylococcus aureus, Listeria monocytogenes	Whole meat, ground beef	H_2S, $(CH_3)_2S_2$, H_2, CO_2, and slime formation due to accumulation of bacterial cells
S. aureus, Acinetobacter, Moraxella	Vacuum packed meats	H_2O_2, H_2S (leads to greening of meat), slime development
Pseudomonas spp., *Shewanella* spp., *Moraxella, Acinetobacter, Bacillus* spp., *Streptococcus*	Fish	Ammonia (NH_3), H_2S, triethylamine, hypoxanthine
Erwinia, *Bacillus* spp., *Clostridium* and *Pseudomonas*	Vegetables	Hydrolyzed polymer, ethyl alcohol, acetic acid, CO_2, H_2, acetoin, alcohol
Erwinia, Xanthomonas, Propionibacterium cyclohexanicum, Gluconoacetobacter spp., *Asaia* spp., *Alicyclobacillus* spp.	Fruits and fruit juices	2-methoxy-phenol, CO_2, H_2, acetic acid
Pseudomonas, Enterobacter, Alcaligenes, spore forming Bacillus and *Clostridium, Flavobacterium*	Dairy products (Raw milk, soft cheese, yogurt, buttermilk, butter)	3 methyl butanol, acetate, H_2, CO_2, ethanol, biogenic amines (biogenic amines may not be the cause of spoilage but can serve as a spoilage index) (Jorgensen *et al*., 2000)
Pseudomonas, Flavobacterium, Acinetobacter, Moraxella, Chromobacterium, Bacillus spp., *Enterobacter* spp., *Klebsiella* spp., *Gluconobacter* spp.	Non-alcoholic beverages (Carbonated and non-carbonated), Alcoholic beverages	2-Ethoxy-3,5-hexadiene, acrolein, ethyl acetate, acetaldehyde

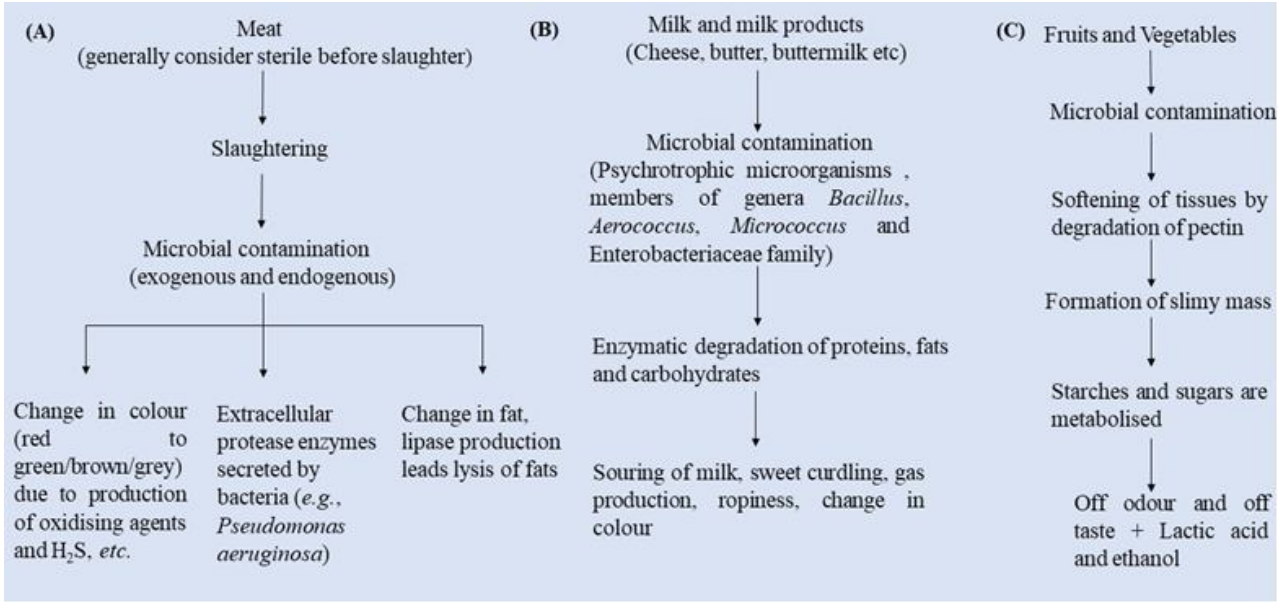


Figure 1: (A) Process of meat spoilage (Pellissery *et al*., 2020), (B) Process of milk and milk products spoilage, (C) Process of fruits and vegetables spoilage.

3. Major foodborne pathogenic bacteria

The American food supply is considered to be the safest in the world, but the federal government estimates that there are around 48 million cases of foodborne illness each year, which means, 1 in 6 Americans becomes sick from contaminated food, which results in an estimated 128,000 hospitalizations and 3,000 deaths (US Food and Drug Administration). Foodborne illness, generally known as food poisoning, is often caused by consuming contaminated food. Not all pathogens have the same potential to cause disease, there are some dangerous strains that cause severe illness. Some major bacteria responsible for foodborne illness are *Campylobacter jejuni*, *Clostridium botulinum*, *Clostridium perfringens*, *E. Coli*, *Bacillus cereus*, *Vibrio* spp. *Salmonella* (2500 types), *Shigella* (30 types) and *Staphylococcus aureus*.

Salmonella is a leading cause of worldwide foodborne infections. In the *Salmonella* group, there are about 2500 different strains (subtypes), but less than 100 strains are known to infect humans. Generally, *Salmonella* lives in the intestines of birds, animals and humans. Most of the *Salmonella* infection occurs due to the consumption of food and water that has been contaminated by faeces (Jumaniyazova and Davranov, 2022). The Food and Drug Administration (FDA) estimates that in the USA every year 79000 cases of foodborne illness occur due to eggs containing *Salmonella*. In humans, infection with *Salmonella* mostly results in, self-limiting diarrhoeal disease, febrile illness and typhoidal fever (enteric fever). Diarrhoeal or febrile illness is caused by non-typhoidal *Salmonella enterica* serovars whereas, enteric fever is caused by *Salmonella enterica* serovars Typhi and *Salmonella enterica* serovars Paratyphi A and B (rarely Paratyphi C). The onset time to symptoms after *Salmonella* infection is approximately 1-3 days (Bintsis, 2017). *Salmonella* spp. are able to colonize and infect the host organisms because of the presence of several pathogenicity islands (PAIs) which encode numerous virulence factors. *Salmonella* pathogenicity island 1 (SPI-1) and *Salmonella* pathogenicity island 2 (SPI-2) are the two chief PAIs that encode two different type III secretion systems which help to deliver effector molecules into the host cell, that result in the internalization of bacteria then lead to systemic spread (Bintsis, 2017).

Most strains of *E. coli* are harmless, not causing disease in humans or animals and living as a part of the normal microbiota of the gut but there are some virulent strains that cause disease (Arbab *et al*., 2022). The virulent strain can cause urinary tract infection, hemorrhagic colitis, sepsis/meningitis, pneumonia, and enteric diarrheal disease. Anyone who comes into contact with a disease-causing strain of *E. coli*. can become infected but, newborns/children, old age people, people with immunocompromised health (*e.g.*, those with diabetes, cancer, HIV and pregnant women) and people who travel frequently to certain countries are more prone to get infected. *E. coli* infections are generally caused by eating improperly cooked food, meat, contaminated fruits, vegetables, sprouts and drinking contaminated (untreated) water, unpasteurized milk or milk products. Virulent or pathogenic strains of *E. coli* have been categorized into six groups according to their pathogenic mechanism (1) Enteropathogenic *E. coli* (EPEC); (2) Enterotoxigenic *E. coli* (ETEC); (3) Enterohemorrhagic *E. coli* (EHEC), also known as Shiga toxin producing *E. coli* (STEC); (4) Enteroinvasive *E. coli* (EIEC); (5) Enteroaggregative *E. coli* (EAggEC); (6) Attaching and Effacing *E. coli* (A/EEC) (Bintsis, 2017; Garcia *et al*., 2010). The disease that is usually associated with EPEC is infantile diarrhoea, which can be mild but the infection sometimes can be severe. EPEC mostly affects developing countries, especially children under age 2. ETEC is highly motile, characterized by the production of several virulence factors such as heat-labile (LT) toxins and heat-stable (ST) toxins along with, various colonizing-factors antigens. It causes gastroenteritis in humans, primarily in infants and is also known as a causative agent of travelers' diarrhoea. ETEC colonizes the small intestine after ingestion and produces toxins to induce fluid secretion.

EHEC is a subset of STEC (Shiga-toxigenic *Escherichia coli*). Serotype O157:H7 is the prototypic EHEC strain, accounting for ~70% of EHEC infections worldwide (U.S. Food and Drug Administration). EHEC is characterized by the production of Stx (Stx1 and /Stx2), the presence of LEE (Locus for enterocyte effacement), a pathogenicity island that encodes for intimin protein that helps in bacterial attachment to epithelial cells, and also several other virulence factors, for example enterohemolysin. EHEC causes hemorrhagic colitis, characterized by severe abdominal pain and bloody diarrhoea. EIEC closely resembles *Shigella*, both of them invade colonic epithelial cells. Symptoms that arise after ingestion of food contaminated with EIEC include abdominal cramps, vomiting, fever, chills, generalized malaise and diarrhoea that often contains blood and mucus.

Campylobacter jejuni is commonly found in animal faeces, water and also associated with poultry (Blaser *et al*., 1980; Szewzyk *et al*., 2000; Hock *et al*., 2023). The cell surface of *C. jejuni* displays various structures, such as the polysaccharides layer also known as capsule, that have an important role in *C. jejuni* biology, especially in host-bacterium interaction (Young *et al*., 2007). This outermost layer of capsular polysaccharides is the main key to virulence, epithelial cell adherence and invasion. *C. jejuni* also produces a cytolethal distending toxin (CDT), which causes cell cycle arrest at G_1/S or G_2/M transition. After *C. jejuni* infection symptoms take 2 to 5 days to develop and last for 1 week. Consuming raw or undercooked poultry meat, unpasteurized milk and contaminated water are the major reasons for campylobacteriosis (Bintsis, 2017). Fever, diarrhoea (often bloody) and stomach pain are the main symptoms that arise after *C. jejuni* infection. In the U.S., each year, *C. jejuni* is responsible for approximately 850,000 illnesses, 8,500 hospitalizations and 76 deaths (Scallan *et al*., 2011).

Bacillus cereus is naturally found in decaying organic matter, the intestinal tract of invertebrates, vegetables, soil, fresh and marine water (Jensen *et al*., 2003; Lotte *et al*., 2022). The spore of *B. cereus* is resistant to extreme environmental conditions such as heat, radiation, drying, and freezing and may be considered as the causative agent of illness (Bottone, 2010). The endospore of *B. cereus* is hydrophobic, which makes it adhesive to multiple types of surfaces. Due to this adhesive nature of endospores, they are frequently found in food production areas and spread to all kinds of food. *B. cereus* produces two types of toxins, the emetic (vomiting) toxin and the diarrhoeal toxin responsible for two types of illness, emetic syndrome and diarrhoeal syndrome. The emetic toxin is produced in food during the growth phase and causes emetic syndrome mainly characterized by nausea and emesis. The diarrhoeal toxin is produced during the growth of bacteria in the small intestine characterized by diarrhoea and abdominal pain (Arnesen *et al*., 2008). During the pathogenicity (intestinal or non-intestinal), *B. cereus* produces tissue-destructive/

reactive exoenzyme, of which four are hemolysins (Gaur *et al*., 2001), three are distinct phospholipases, an emesis-inducing toxin and three pore-forming enterotoxins (1) Hemolysin BL (2) Non-hemolytic enterotoxin (3) Cytotoxin K (Lund and Granum, 1997; Lund *et al*., 2000; Saki *et al*., 2001). Out of all food poisoning breakouts, *B. cereus* is estimated to be responsible for 1.4-12 %. (Grutsch *et al*., 2018). Approximately, 63000 cases of food poisoning are caused by *B. cereus* every year in the U.S. (Carroll *et al*., 2019). Nausea, vomiting, diarrhoea and abdominal pain are the main symptoms that arise after *B. cereus* infection and have an incubation time of 8-16 h, also known as the 'long incubation' form of *B. cereus* (Todar, 2009).

Staphylococcus aureus usually does not cause any infection but it can also become an opportunistic pathogen when it is allowed to enter the bloodstream and internal tissues (Lowy, 1998). It can cause skin and soft tissue-related infections such as abscesses, carbuncles, scalded skin syndrome and also has the potential to cause septic arthritis, pulmonary infections like pneumonia, urinary tract infections, bacteremia, gastroenteritis and toxic shock syndrome. TSS Toxin-1 or TSS-1, an exotoxin which is secreted as a single polypeptide by *S. aureus* resulting in Toxic Shock Syndrome causes inflammation, fever and shock. The human body is the major reservoir of *S. aureus* which can spread by direct or indirect contact, through respiratory tract droplets. Inadequate cooking, inadequate refrigeration and lack of personal hygiene can be the reasons for staphylococcal contamination of food, ingestion of food contaminated with *S. aureus* leads to food poisoning. About nine staphylococcal enterotoxins are identified, out of which type A and type D are responsible for the majority of outbreaks (Mossel *et al*., 1995). The incubation period is less than 6-10 h after the ingestion of staphylococcal enterotoxin and the symptoms that may arise include, nausea, vomiting, headache, abdominal pain, general weakness, muscle cramps, dizziness, chills and diarrhoea (may or may not be bloody) (Bacon and Sofos, 2003).

Clostridium botulinum occurs extensively in soil, untreated water, seawater, sediments of oceans and lakes as well as in the intestinal tract of animals. *C. botulinum* and its related species produce a neurotoxin called botulinum toxin or botulinum neurotoxin (BoNT), one of the most naturally occurring poisonous substances known, which causes botulinum, an acute and flaccid paralysis. There are seven distinct forms of neurotoxins (BoNT), designated, types A, B, C, D, E, F and G, based on the antigenic specificity of the toxin produced by each strain (Bintsis, 2017). Type A, B, E and rarely F toxins caused foodborne botulism outbreaks in humans and type A toxin were reported to be more lethal than type B and E (Boerema and Broda, 2004). Types C and D are not associated with human disease, they cause botulism in other animals as well as birds and type G, has yet to be clearly implicated in a botulism case (Murray *et al*., 1999). In humans, types A, B and E are associated with foodborne illness whereas type E is specifically associated with fish or fish products. *C. botulinum* is also classified into four different phenotypic groups, *i.e*., group I-IV. Group I contains all strains of type A, proteolytic strains of type B and F, and dual toxin types AB, AF and BF, which show best growth at 37°C and produce spores even with high heat resistance (112°C); group II contains strains of type E and non-proteolytic strains of type B and F, grow best at 30°C or less (psychrotrophic) and produce spores with low heat resistance (80°C); group III comprise of strains producing type C or D toxin and are non-proteolytic, grow optimally at 40°C and have spores with intermediate heat resistance (104°C); group IV strains produce type G toxin, are asaccharolytic (unable to metabolize carbohydrates), grow optimally at 37°C and spores heat resistance is intermediate (104°C) (Collins and East, 1998).

Foodborne botulism is caused by consuming food and beverages contaminated with the toxin such as prepared home-canned foods (mushroom, asparagus, beets, peppers, green beans), stored food products (garlic in oil, commercially prepared cheese sauce, baked potato wrapped in aluminium foil stored at room temperature, onions sauteed in butter) and traditionally prepared fish or marine mammal meat. Botulinum toxin can also affect infants, most commonly it affects 3 weeks to 6 months old babies, but babies are at higher risk until they are 1 year old. Infant botulism is also associated with food, such as, honey, that also can contain spores of *C. botulinum* that germinate, colonize and produce neurotoxin in the infant's intestinal tract and for this reason, honey is not recommended for infants less than 12 months old. Generally, the symptoms of botulinum neurotoxin ingestion appear after 12-36 h and primarily may include nausea, weakness and vertigo. However, these symptoms are followed by visual imparts (blurred or double vision), flaccid paralysis, lack of muscle coordination, difficulty in speaking and swallowing due to dry mouth, throat and tongue as well as sour throat, and difficulty in breathing.

Clostridium perfringens is commonly found in the intestinal tract of humans and animals (domestic as well as wild), and also in nature including soil, water, sediments and area subjected to human and animal faecal pollution. It is estimated to be the second most common bacterial cause of foodborne illness in the U.S., causing around one million cases of illness every year (Grass *et al*., 2013). *C. perfringens* produce various types of toxins in several different combinations such as CPA (alpha toxin), CPE (entero-toxin), ETX (epsilon toxin), ITX (iota toxin), PFO (perfringolysin or theta toxin), CPB (beta toxin) and CPB2. The two major toxins which are directly associated with foodborne disease in humans are CPB and CPE. *C. perfringens* requires amino acids because it lacks the ability to produce 13 out of 20 essential amino acids and vitamins for its growth. It acquires the required amino acids by breaking down host tissues, through using its digestive enzymes and toxins. *C. perfringens* is most commonly found in red meat (beef, pork), gravis, poultry (chicken, turkey) and less commonly in fish and vegetables and contaminates food when it is undercooked or not refrigerated properly. After ingestion of contaminated food, the vegetative cells of *C. perfringens* probably die when exposed to stomach acid but some remain alive and enter the small intestine where they multiply, sporulate and release toxin (CPE). This entero-toxin (CPE) induces intestinal tissue damage, abdominal cramps and intestinal fluid loss (clinically manifests as diarrhoea) (Doyle *et al*., 2019). Besides food poisoning, *C. perfringens* strains also cause other diseases such as myonecrosis (gas gangrene), clostridial cellulitis, gangrenous cholecystitis, postabortion infection, pneumonia, intravascular hemolysis and bacteremia, *etc*.

Shigella spp. is also known to survive for extended periods of time under frozen (-20°C) or refrigerated conditions (4°C) and *S. sonnei* is able to bear lower temperatures better than other serogroups (Lightfoot, 2003; Warren *et al*., 2006; Bintsis, 2017). *Shigella* spp. are the members of the Enterobacteriaceae family, they are closely related to the genus *Escherichia* in their DNA homology. Nucleotide sequencing of several conserved genes has shown that *Shigella* emerged

from *E. coli* and it has also been postulated that *Shigella* spp. directly evolved from commensal *E. coli* lineages, but the modern taxonomy revealed that enteroinvasive *E. coli* strains were more closely related to *Shigella* spp. than to commensal *E. coli* (Doyle *et al*., 2019). *Shigella* is one of the leading bacterial causes of diarrhoea worldwide and humans are the only host of it. It is commonly found in environments of compromised hygiene and cause shigellosis. The primary route of transmission is through person-to-person contact, shigellosis also occurs by consuming contaminated raw or processed food and water. Food can become contaminated when it is handled by an infected person who does not take proper care of hygiene or if contaminated water is used for growing fruits and vegetables. A number of raw or undercooked foods have been linked to shigellosis for example; salads (tuna, potato, shrimp, tofu, eggs, chicken and macaroni), lettuce, tomato, five-layer (beans, salsa, guacamole, nacho cheese and sour cream) party dips, raw baby corn and unpasteurized milk and milk products. *Shigella* spp. can infect anyone, but 1-4-year-old children, elderly persons and immunocompromised individuals are at higher risk of infection.

Vibrio spp. grow over a wide range of temperatures (20 to>40°C) and are naturally found in estuaries, seawater and fresh water. The most common pathogenic *Vibrio* spp. are, *Vibrio cholerae*, *Vibrio parahaemolyticus* and *Vibrio vulnificus*. Infections due to *Vibrio* spp. are majorly initiated by consumption of raw or undercooked contaminated seafood and exposure to contaminated water. The etiologic agent of cholera is *Vibrio cholera*, which causes a severe illness of diarrhoea usually caused by ingestion of contaminated food and water. It is estimated that, worldwide every year around 3-5 million people are infected by *Vibrio cholera* (D'Mello-Guyett *et al*., 2020). *Vibrio cholera* can also be found in freshwater as free-living or in association with planktons or in the form of biofilm. It is transmitted through faecal-oral mode by drinking contaminated water and can also be transmitted *via* person-to-person close contact (Goh *et al*., 1990; Rabbani and Greenough, 1999; Sugimoto *et al*., 2014). There are more than 200 serogroups of *Vibrio cholera,* distinguished on the basis of the chemical composition of the O-antigen of lipopolysaccharide (LPS), but most of the cholera cases are caused by serogroup O1 and O139. O1 and O139 serogroups of *Vibrio cholera* produce an enterotoxin called cholera toxin (CT), that causes mild to severe diarrhoea. In the U.S., sources of infection with these organisms have been associated with the ingestion of contaminated food, seafood (molluscan fish, crab, shrimp, squid, lobster and finfish) and contaminated water. All people are susceptible to cholera but, people who are living in poorly developed areas and areas with high population density, are more likely to get infected.

V. parahaemolyticus is frequently isolated from the estuaries and sea of the United States and other tropical-to-coastal areas, worldwide. *V. parahaemolyticus* is halophilic, it is lysed immediately in freshwater; therefore, it is not transmitted through the faecal-oral route (U.S. Food and Drug Administration). Generally, most *V. parahaemolyticus* isolates are non-pathogenic but, currently, pathogenic strains are identified by the presence of one or both of the hemolysin, *i.e*., thermostable direct hemolysin (TDH) and thermostable related hemolysin (TRH). TDH is a pore-forming toxin, it lyses red blood cells and attacks intestinal cells to disrupt the electrolyte balance. TRH toxin also works in the same way, disrupting electrolyte flux in intestinal cells. *V. vulnificus* is the natural flora of estuaries and coastal marine environments, worldwide. *V. vulnificus* strains are classified into biotypes on the basis of their biochemical characteristics. Strains of biotype 1 cause the majority of human infections, whereas strains of biotype 2 are eel pathogens and biotype 3 strains possess biochemical properties of both biotype 1 and biotype 2, causing human wound infection (Velez *et al*., 2023). *V. vulnificus* infection occurs due to the consumption of various contaminated seafood including fish, oysters, shrimp and clams. It can result in a severe, fulminant systemic infection characterized by fever, nausea, chills, hyposensitive septic shock and formation of secondary lesions on the extremities of the infected individual (Bowdre *et al*., 1983; Chuang, *et al*., 1992).

4. Impact of foodborne pathogens on human health

Consumption of safe, healthy and nutritious food is important for good health. Food contaminated with microbes, parasites and chemical agents can cause various diseases from diarrhoea to cancer. It was Hippocrates (460 B.C.) who reported that there is a very close connection between the food we consume and human illness (Hutt and Hutt, 1984). A foodborne outbreak occurs when two or more cases of similar illness arise by consuming common food or when the observed number of cases of a particular disease exceeds the expected number (Bintsis, 2017). Foods that are associated with foodborne illness are majorly of animal origin, particularly eggs and eggs products, milk and dairy products, broiler meat, fish and fish products, however, fruits and various vegetables are also recognized as a source of foodborne outbreaks in many parts of the world. In the USA, outbreaks associated with leafy vegetables have been higher than outbreaks associated with other food types (Yang *et al*., 2017). Over the past 10 years, the topmost culprits linked with the foodborne outbreaks were, *Salmonella* spp., *Listeria monocytogenes*, and *E. coli* (*E. coli* O121, *E. coli* O157:H7, *E. coli* O103, *E. coli* 26, *E. coli* O157, *E. coli*. 145). From 1973 to 2012, STEC was linked to 18% of leafy-vegetables-associated outbreaks (Herman *et al*., 2015). In 2011, between the months of May and July, as well as in June of the same year, there was an outbreak of Shiga-toxin-producing *E. coli* (STEC) in the EU. More than 3,100 cases of bloody diarrhoea and about 850 cases of hemolytic uremic syndrome (HUS), were reported across the EU. *Via* Epidemiological investigation, contaminated raw sprouts were identified as the most probable source of the illness (European Food Safety Authority, 2012). In 1982, the O157:H7 serotype of *E. coli* caused two outbreaks of disease, that were associated with the consumption of undercooked ground meat. On January 6, 2022, the CDC (Centre for Disease Control and Prevention) and FDA (US Food and Drug Administration) reported an outbreak of *E. coli* O157:H7 serotype linked to packaged salad. This outbreak affected four states of the USA including, Washington, Alaska, Ohio and Oregon, in which, 10 individuals became ill and 4 were hospitalized as per the CDC report. In India, from 2009-2018 total of 2688 foodborne disease outbreaks with 153,745 illnesses and 572 deaths were reported to IDSP (Integrated Disease Surveillance program).

Salmonella spp. is also the leading cause of bacterial foodborne outbreaks, worldwide. A recent report from CDC estimates that, in the USA, approx. 1,027,561 cases of domestically acquired non-typhoidal salmonellosis occur every year. In 2021, the FDA, along with the CDC, investigated a foodborne outbreak of *Salmonella* Oranienburg infections linked to whole, fresh onion. CDC reported that 39 states of the USA were affected along with, 1040 illnesses and 260 hospitalizations. After analysis of outbreak data from 1998-2008, it is estimated that beef is the third-most common source of bacterial foodborne illness in the USA and the fourth-most common

source of *Salmonella* outbreak after poultry, eggs and pork (Gould *et al*., 2013). Consumption of *Listeria monocytogenes* contaminated food causes a serious illness called, listeriosis and it is also one of the leading causes of death from foodborne pathogens, especially in newborns, pregnant women, old age people and people with compromised immune systems (Buchanan *et al*., 2017). In 2015, 26 member states of EU, reported 2,206 confirmed cases of listeriosis. EFSA reported that in 2013, 1763 confirmed cases of listeriosis in humans were reported in 27 member states (EFSA, 2015). The vast majority of cases were reported to be domestically acquired and implicated food vehicles were, meat and meat products, cheese, seafood, vegetables and juices (Buchanan *et al*., 2017).

5. Lactic acid bacteria and its genera

Lactic acid bacteria (LAB) belong to the phylum Firmicutes, class Bacilli and order Lactobacillales. LAB are catalase-negative, non-sporing and non-respiring, which means they do not require oxygen for oxidation of respiratory substrates (carbohydrates, fats, proteins, organic acids), and during the fermentation of carbohydrates, they produce lactic acid as a major end product (Mokoena *et al*., 2021; Pandey and Yadav, 2022). They are usually non-motile and have low GC content in their DNA, *i.e*., less than 55 mol % and this separated these traditional lactics from the bifidobacteria which have more than 55 mol % GC content in the DNA (Stiles and Holzapfel, 1997). Four genera of LAB; namely, *Leuconostoc*, *Pediococcus*, *Lactobacillus* and *Streptococcus*, were originally described, but recent taxonomic revision have suggested the inclusion of new genera, *Aerococcus*, *Alloiococcus*, *Carnobacterium*, *Dolosigranulum*, *Enterococcus*, *Globicatella*, *Lactococcus*, *Oenococcus*, *Tetragenococcus*, *Vagococcus* and *Weissella* (Mozzi, 2016). LAB can be divided into two groups, *i.e*., homofermentative and heterofermentative, on the basis of the end product they form during the fermentation of glucose. Homofermentative LAB including, *Pediococcus, Streptococcus, Lactococcus*, *Enterococcus* and some *Lactobacillus* species produce lactic acid as a major end product of glucose fermentation, on the other hand, heterofermentative LAB including, *Weissella, Leuconostoc, Oenococcus* and some *Lactobacillus* species produce the equimolar amount of lactate, CO_2 and ethanol from glucose fermentation.

The *Streptococcus* genus is heterogenous and also one of the original genera of LAB. *Streptococcus thermophilus* species used, together with *Lactobacillus delbrueckii* subsp. *Bulgaricus* for the production of yogurt, is also found in many fermented milks along with other LAB and used as a starter culture in the production of various Italian cheeses (Narvhus and Axelsson, 2003). The *Lactococcus* genus is also one of the important genera of LAB, they are an important part of commercial dairy starter cultures used for the production of sour creams, fermented milk and a variety of cheese. *Tetragenococcus halophilus* species of *Tetragenococcus* genera are important in the fermentation of soy sauce, miso and fish sauce. Production of pickles, sauerkraut and fermented olives done by *Pediococcus* and other LAB including *Leuconostoc, Enterococcus* and *Lactobacillus*. Multiple strains of LAB are also used as probiotics. Probiotics are basically a combination of live microorganisms when administrated in the host in an adequate amount, provide health benefits by improving gut microflora. Genera of LAB that have been used as probiotics are *Lactobacillus*, *Leuconostoc*, *Pediococcus* and *Streptococcus*. Probiotics interact with pathogenic bacteria and inhibit their growth through the production of antimicrobial compounds (Khaneghah *et al*., 2020).

6. Antimicrobial compounds produced by LAB and their role against foodborne pathogenic bacteria

Nearly, 99% of studied foodborne pathogens have a wide range of defensive mechanisms like the production of antibiotics, lytic agents, bacteriocins and proteins in the form of toxins. On the other way, LAB are also capable of displaying antimicrobial activities in fermented food due to the production of various compounds such as organic acids, acetaldehyde, bacteriocins, ethanol, hydrogen peroxide, reuterin and diacetyl. LAB are the important component in various food industries, food that contain LAB has probiotic and antimicrobial properties, that help in the prevention of infectious disease in human. These bioactive compounds produced by microorganisms were referred to as postbiotics by Langella and Martin (2019). LAB and its by-products are classified as Generally Recognised as Safe (GRAS) by the U.S. Food and Drug Administration.

6.1 Bacteriocins

Bacteriocins are ribosomally synthesized heat-stable antimicrobial peptides. Almost all strains of LAB's genera are capable of producing bacteriocins. Since bacteriocins are isolated from foods like fermented vegetables, meat and dairy products, which ordinarily contain LAB, they have been eaten for millennia without people being aware of it. LAB bacteriocins remain active at a wide range of pH and also show tolerance towards high-thermal stress. Bacteriocins are currently the focus of research and the food industry communities due to their potential for use as natural bio-preservatives to increase food shelf-life and suppress the growth of foodborne pathogens during farming and food processing procedures (Perez *et al*., 2014). Food spoilers like *Clostridium* spp. and foodborne pathogens including *Listeria monocytogenes*, *Staphylococcus* spp., *Bacillus* spp., *Clostridium*, and *Enterococcus* are key targets of bacteriocins. According to the Klaenhammer (1993) categorization method which was further modified (Nes *et al*., 1996), bacteriocins of LAB are grouped into four classes (Figure 2).

Bacteriocins act very fast, even at low concentrations, they form pores in the targeted bacterial membrane and due to their proteinaceous nature, they are easily degraded by proteases produced in the gastrointestinal tract of humans, consequently, their fragments do not live long in human body (Perez *et al*., 2014; Kiran *et al*., 2021). The prime target of bacteriocins is the cell membrane of bacteria (Figure 3) and because of the protective layer of LPS in Gram-negative bacteria, they act more effectively against Gram-positive bacteria (Ray, 1993; Sahl *et al*., 1995). Some bacteriocins, such as colicin E2, E3, and megalin A-216, exhibit antimicrobial action through enzymatic activities like DNase, RNase, and phospholipase, respectively (Aljohani *et al*., 2023). The bacteriostatic activity of bacteriocins is affected by various factors, including dosage, level of purification, growth phase, pH, temperature, and the presence of other antimicrobial substances that can alter cell wall integrity (Bhattacharya *et al*., 2022). Nisin, pediocin PA-1 and micocin are well-known bacteriocins produced by LAB and are approved by the USFDA for commercial use (Aljohani *et al*., 2023).

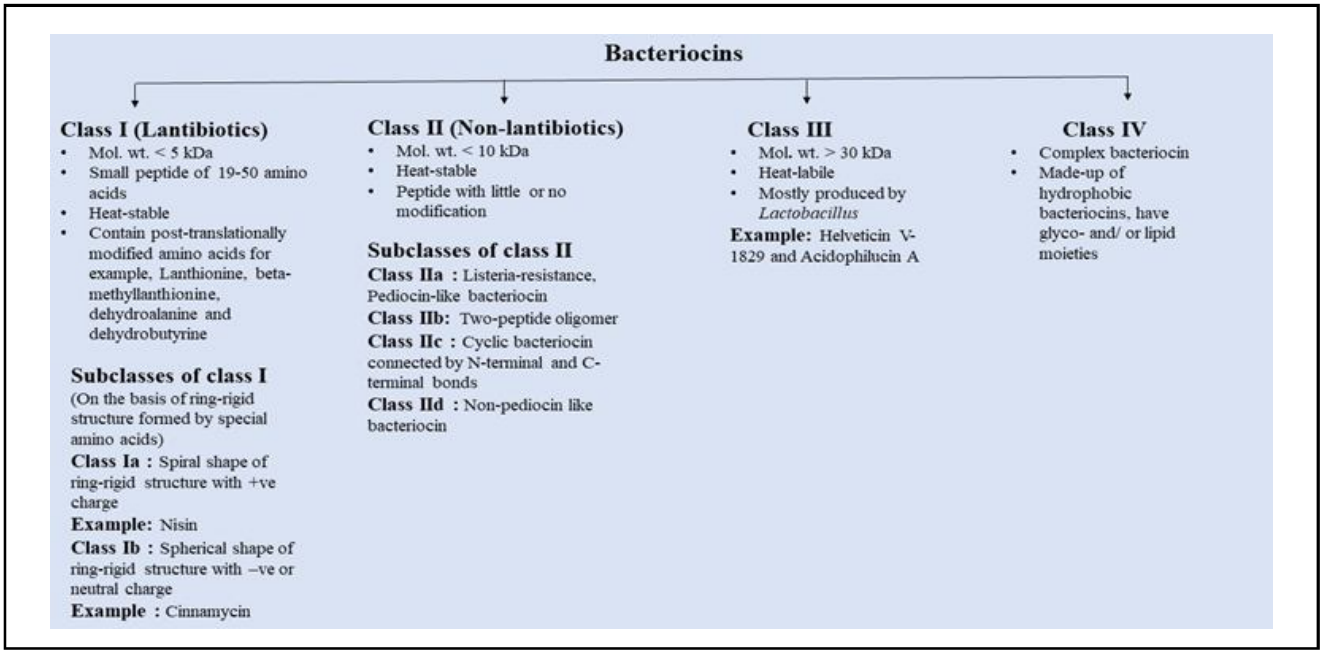


Figure 2: Classification of LAB bacteriocins (Jiang, 2021).

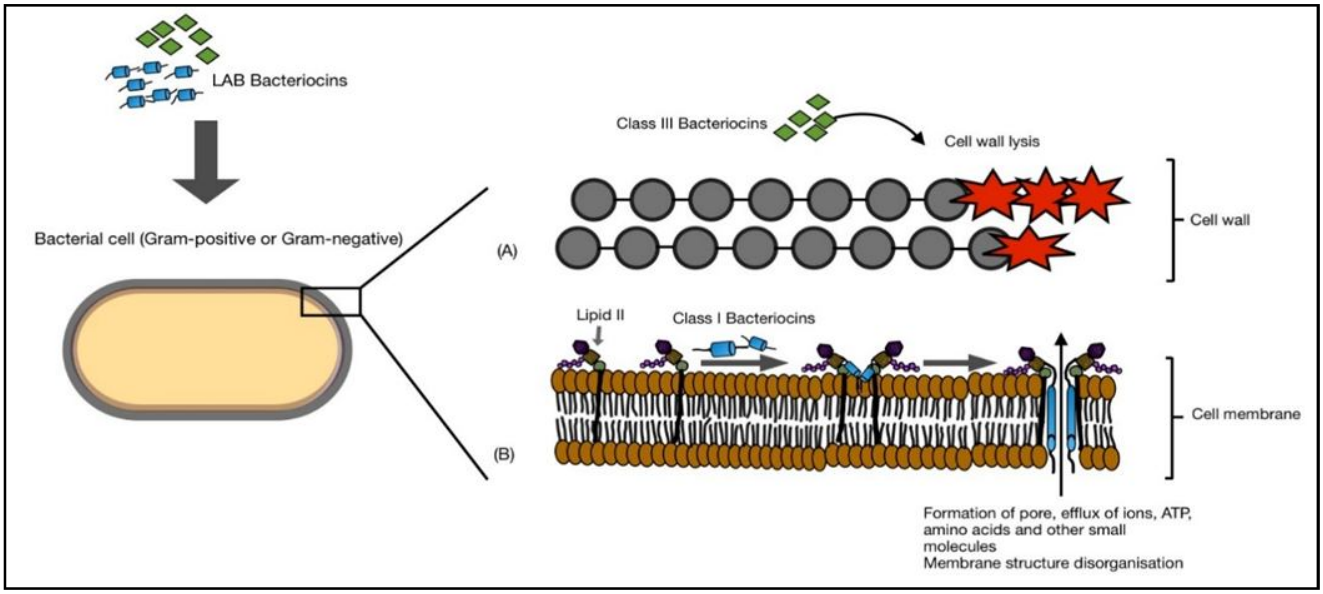


Figure 3: Action of LAB bacteriocins on bacterial cell.

(A) Class III bacteriocins (especially class IIIa) target bacterial cell wall and cause direct cell wall lysis and death (B) Class I bacteriocin (*e.g.*, Nisin) binds with membrane-bound peptidoglycan precursor lipid II, resulting in inhibition of peptidoglycan synthesis. The nisin-lipid II complex forms pores in the bacterial cell membrane which leads to the efflux of intracellular ions, ATP, amino acids and other molecules that ultimately cause cell death.

6.2 Organic acids, acetaldehyde and ethanol

During the lactic acid bacterial fermentation of food, a variety of organic acids including, acetic acid, lactic acid and propanoic acid are produced. Organic acids exert a direct antimicrobial effect on food spoilage and foodborne pathogens. However, these acids do not show similar/equal antimicrobial activity at a given molar concentration. They provide an acidic environment that does not favour the growth of pathogenic microorganisms. The antagonistic action of these organic acids causes, interference with the maintenance of membrane potential, inhibition of active transport, reduction of intracellular pH and inhibition of various metabolic functions (Caplice, 1999). Acetaldehyde is an aroma compound in yogurt and other dairy industries but it makes a very small contribution to bio-preservation because the flavour threshold is much lower than the amounts thought to be required to achieve microorganism inhibition (Kulshrestha and Marth, 1974). Similar to this, the amount of ethanol produced in the food system is so low that the contribution to antibiosis is negligible (Caplice, 1999).

6.3 Carbon dioxide

During heterolactic fermentation, CO_2 is formed which directly creates an anaerobic environment that is toxic to some aerobic bacteria that are spoiling food (Eklund, 1984). The inhibitory action of CO_2 on the bacterial cells depends on the permeability of the cells. Shaughnessy and Winslow (1927) state that, the permeability of *Bacillus cereus* is much greater than that of *Bacterium coli*. So, according to this observation, *Bacterium coli* is resistant to high concentrations of CO_2, whereas *Bacillus cereus* is more susceptible (Coyne, 1933). CO_2 also has the ability to reduce the external and internal pH of the bacterial cell.

6.4 Diacetyl

Diacetyl is a water-soluble and volatile compound produced by the metabolism of sugars *via* pyruvate. It has a buttery odour and is responsible for the flavour and aroma particularly, of butter and other milk products such as cheese, milk and yogurt (Schaeffer and Iannucci, 2014). Production of diacetyl decline in the presence of lactate, increase in temperature from 21-30°C and increase in pH, however production increase when there is the presence of metal ions (Cu^{++}, Mg^{++}or Mn^{++}), aeration or addition of hydrogen and catalase to milk (Dillon, 2014). Many strains of LAB's genera including *Lactococcus, Leuconostoc, Lactobacillus* and *Pediococcus* may produce diacetyl. Diacetyl acts as an antimicrobial when present in high concentrations. Gram-negative bacteria are more sensitive to diacetyl than Gram-positive bacteria.

6.5 Hydrogen peroxide

H_2O_2 produced during aerobic growth, inhibits bacterial respiration, growth, and viability. H_2O_2 is referred to as a biocide because it quickly and effectively kills bacteria by causing extremely harmful DNA damage. Metabolite like the hydroxyl radical, which is produced when H_2O_2 and superoxide react, is responsible for its bactericidal characteristic. Particularly, H_2O_2 can have a significant oxidizing effect on membrane lipids and cellular proteins. Moreover, the formation of hypothiocyanate and other antimicrobials by H_2O_2 may trigger the lactoperoxidase system in fresh milk (Reiter and Harnulv, 1984).

6.6 Reuterin

Reuterin (3-hydroxypropionaldehyde) is a non-proteinaceous, water-soluble antimicrobial compound with low molecular weight. It is a mixture of different forms of 3-hydroxy propionaldehyde (3-HPA) (Talarico and Dobrogosz, 1989). Reuterin has broad-spectrum antimicrobial activity and shows antagonistic effects against yeasts, molds, protozoa, Gram-positive and Gram-negative bacteria. Certain heterofermentative *lactobacilli* (*e.g.*, *Lactobacilli reuteri*) produce reuterin during anaerobic metabolism (in stationary phase) of glycerol or glyceraldehyde. With or without the addition of glycerol, reuterin or reuterin-producing *lactobacilli* can be used to manage food spoilage and pathogenic microorganisms in food (Dillon, 2014). The antimicrobial activity of reuterin is thought to be due to inhibition of ribonucleotide reductase (Dobrogosz *et al*., 1989). Reuterin has the ability to inhibit the growth of *E. coli*, *Salmonella* spp., *Clostridium*, *Shigella*, *Listeria* as well as *Staphylococcus*. More recently, an antibiotic reutericyclin was discovered, which is produced by strains of *Lactobacilli reuteri* isolated from sourdough. Reutericyclin is highly hydrophobic and negatively charged and the cytoplasmic membrane was proposed as its cellular target in research on its mode of action (Ganzle and Vogel, 2003). This antibiotic is very effective against Gram-positive bacteria and it also inhibits the growth of pathogenic bacteria *Staphylococcus aureus*, *Listeria innocua*, as well as the opportunistic pathogen *Enterococcus faecium* (Ganzle, 2004).

7. Conclusion

In today's world, the spreading of food pathogens in the complex food supply system has been a serious public health concern. The food industries use various methods to control microbial growth including heat sterilization and the addition of synthetic/artificial preservatives. However, using these methods can cause a series of undesirable consequences such as the destruction of nutritional content, generation of chemical residues, fading of flavours and taste as well as speeding up the variation of resistant strains. Bio-preservation may provide a substitute for chemical and physical methods of food preservation, which are typically viewed as detrimental to product quality as well as detrimental to health in some cases. Consequently, food industries have recently shifted towards safer methods of microbial growth control by considering consumer health concerns into account. Biofilms, the major concern of food industries are also being tackled by using numerous safer methods like the usage of enzymatic disruption (cellulases, proteases, glycosidases), and steel coating with various nanoparticles and essential oils.

The LAB falls under the category of GRAS and they are widely used in food industries. Besides their ability to enhance the flavour and texture of the food, LAB and their metabolites are able to control microbial growth and are in use for the same. Nisin, pediocin-PA1 and micocin are the only FDA-approved bacteriocins that are used as bio-preservatives in food industries, so to understand the action mechanism and the bio-preservative potential of other bacteriocins, thorough research is important. Bacteriocins are a very effective solution for food product preservation because they have no flavour, no aroma, no colour and they preserve the nutritional value of food items. Further, the lactic acid-H_2O_2 consortium displayed enhanced killing activity to pathogenic bacteria. So, besides bacteriocins, other metabolites and their combination would be a promising antimicrobial agent in food production processes.

Acknowledgements

Authors acknowledge the facilities provided by Department of Biotechnology, Himachal Pradesh University, Shimla. Anupam Sharma and Vikrant acknowledge Junior Research Fellowship from CSIR, New Delhi and Priyanka acknowledges Junior Research Fellowship from UGC, New Delhi.

Conflict of interest

The authors declare no conflicts of interest relevant to this article.

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Citation **Anupam Sharma, Vikrant, Priyanka and Wamik Azmi (2023). Antimicrobial potential of lactic acid bacteria against food spoilage and foodborne pathogenic bacteria. Ann. Phytomed., 12(2):120-130. http://dx.doi.org/10.54085/ap.2023.12.2.14.**