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Review

Inhibitory Effect of Lactic Acid Bacteria on Foodborne Pathogens: A Review

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ABSTRACT

Foodborne pathogens are serious challenges to food safety and public health worldwide. Fermentation is one of many methods that may be used to inactivate and control foodborne pathogens. Many studies have reported that lactic acid bacteria (LAB) can have significant antimicrobial effects. The current review mainly focuses on the antimicrobial activity of LAB, the mechanisms of this activity, competitive growth models, and application of LAB for inhibition of foodborne pathogens.

Key words: Antimicrobial action; Competitive growth models; Foodborne pathogens; Lactic acid bacteria; Preservation; Preservative

Foodborne pathogens have become important social topics and have received much attention from consumers and food safety regulatory agencies around the world because of frequent outbreaks of microbial infections. For example, an outbreak of *Listeria monocytogenes* serotype 4b infection was reported in 1985 in California *(55)*. The outbreak was associated with consumption of contaminated Mexican-style cheese and resulted in 142 cases of human listeriosis. In 2006, a single strain of genotype GII/4 norovirus caused 118 infections in Kobe, Japan *(43)*. Peppers contaminated with *Salmonella* Saintpaul led to 1,442 illnesses, 2 deaths, and 286 hospitalizations in 43 states in the United States and Canada in 2008 *(69)*. An outbreak of Shiga toxin–producing *Escherichia coli* O141: H4 infection caused 3,816 illnesses and 54 deaths in 2011 in Germany, and the infection was spread to 15 countries in Europe and North America by people traveling to Germany at that time *(30)*. From 2006 to 2015, 2,868 food safety–related incidents occurred in China, involving 94,979 people *(105)*. A report released by the Chinese National Health and Family Planning Commission on Microbial infection indicated that microbial infection was the largest contributor (1,118 incidents, 39.0% of the total) and affected 58,184 people, which accounted for 61.3% of the food safety incidents; the other 38.7% was mainly caused by physical and chemical pollution.

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Fermentation has a history of thousands of years and has been used for long-term food preservation *(57, 58, 111)*. Lactic acid bacteria (LAB) are the most important microorganisms associated with fermentation. These non-sporulating gram-positive bacteria are widely distributed in nature. Their main product is lactic acid, which is produced as they ferment carbohydrates. LAB utilize and convert carbohydrates, primarily glucose, in the raw materials to produce various metabolites, which give the food its unique flavor and nutritional value and are not present before fermentation *(78)*. Many LAB have probiotic properties and antimicrobial effects *(4, 61, 71),* suggesting that LAB can be used in food preservation.

This article is a review of the antibacterial activity of LAB against several common foodborne pathogens in various media and introduces the potential application of these LAB in the food industry. The article also includes a brief introduction to the use of competitive growth modeling with LAB and a discussion of the characteristics of LAB that can be exploited to inhibit pathogens.

INHIBITION OF FOODBORNE PATHOGENS BY LAB

In previous studies, LAB had a wide range of antimicrobial effects against many foodborne pathogens *(28, 62, 93, 126)* that may cause various gastrointestinal diseases or even death in humans. However, particular levels of LAB were needed before interactions with pathogenic bacteria could be initiated. When LAB levels

reached the appropriate threshold, bacteriostatic metabolites were released in concentrations sufficient to inhibit the growth of harmful bacteria. However, when these conditions are not met, replication of pathogenic bacteria will be almost unaffected. After coinoculating *Lactobacillus casei* and *L. monocytogenes* in a 10:1 ratio, Pálmai and Kiskó *(72)* found that *L. monocytogenes* attained a higher population than did *L. casei* at 7, 13, and 20°C. However, when the *L. casei*/*L. monocytogenes* ratio was increased to 100:1 or 10,000:1, an inhibitory effect on *L. monocytogenes* was observed. The mechanisms by which LAB inhibit pathogenic bacteria remain unclear. However, the ability of LAB to produce organic acids, hydrogen peroxide, and bacteriocins is believed to be responsible for the antimicrobial activity.

L. monocytogenes. *L. monocytogenes* is ubiquitous in the environment and is highly resistant to extremes of pH and temperature. This pathogen can survive under adverse conditions in many kinds of food and has been found in numerous foods such as meat, eggs, poultry, seafood, dairy products, fruits, and vegetables *(15, 32, 80, 84)*. *L. monocytogenes* can reproduce under refrigeration (4°C) *(46)* and can contaminate frozen and ready-to-eat foods. Consumption of food contaminated by *L. monocytogenes* may cause severe health problems, and many countries have a zero-tolerance policy for this pathogen in ready-to-eat foods.

In 1988, Schaack and Marth *(87)* pointed out that the growth of *L. monocytogenes* was inhibited by *Lactobacillus bulgaricus* and somewhat inhibited by *Streptococcus thermophilus*. Because *L. monocytogenes* is a major hazard to human health, methods for its effective control in food have been studied extensively. Hundreds of studies regarding the interaction between LAB and *L. monocytogenes* in various media and with various LAB strains have been performed, and in all cases LAB inhibited the growth of *L. monocytogenes* (Table 1) *(97, 121, 125)*.

Staphylococcus aureus. *S. aureus* is a gram-positive coccal bacterial species that is widely distributed in the environment. It can be found on the skin, in the nares, or on pharyngeal surfaces in 25 to 30% humans and can cause invasive infections *(66, 109)*. The Centers for Disease Control and Prevention reported that *S. aureus* is the most common foodborne pathogen *(23)*. The emergence of methicillin-resistant *S. aureus* has resulted in extensive work by researchers to find ways to inhibit and inactivate this pathogen.

Many microorganisms can repress the growth of *S. aureus*. DiGiacinto and Frazier *(25)* tested the effects of coliform and *Proteus* cultures on the growth of *S. aureus,* mostly strains from food. The examined cultures somewhat inhibited *S. aureus,* and the effects were enhanced by increasing the proportions of these bacteria. However, Kao and Frazier *(48)* obtained a mixed result when LAB were cocultured with *S. aureus*. Some LAB promoted growth of *S. aureus* under all conditions, whereas others promoted *S. aureus* growth only at high temperatures. Some strains inhibited *S. aureus* multiplication consistently, whereas others inhibited the pathogen only at low temperatures. More recent studies also have been conducted to evaluate on the inhibitory activity of LAB against *S. aureus*. Kang et al. *(47)* found that both *Lactobacillus salivarius* and *Lactobacillus fermentum* effectively inhibited six *S. aureus* strains, including three methicillin-resistant strains (Table 2).

Salmonella. *Salmonella* is a common enteropathogen. Poultry are considered the most common carrier of this pathogen, but it can also be present in contaminated water and foods due to inadequate hygienic and sanitation practices *(82)*. Salmonellosis, whose sequelae can include gastroenteritis, typhoid, and paratyphoid clinical signs, is one of the most significant zoonoses for public health *(39, 124)*. Therefore, a valid program that addresses *Salmonella* contamination in food is needed urgently.

Many researchers have found that LAB can have an inhibitory effect against *Salmonella (50, 114, 118),* and the bacteriostatic substances produced by LAB are thermally stable (Table 3). The main bacteriostatic factor probably is the low pH caused by LAB fermentation. These discoveries are crucial for addressing the problem of foodborne salmonellosis.

E. coli. *E. coli* is a gram-negative brevibacterium that is widespread in nature and can be found in the intestinal tracts of humans and animals. This bacterial species was once considered generally nonpathogenic, and researchers believed that it caused diarrhea only under certain conditions. However, this pathogen became a public health concern after the first outbreaks of foodborne illness associated with enterohemorrhagic *E. coli* O157:H7 were reported in Oregon and Michigan in 1982 *(49, 107)*. As the dominant cause of hemorrhagic colitis and hemolytic uremic syndrome, *E. coli* O157:H7 is known as an important human pathogen and has been identified as the causative agent in various outbreaks, with at least 20,000 infections and death each year *(123)*. The low infectious dose and the ability to secrete Shiga toxin–like substances make *E. coli* O157:H7 one of the most serious known foodborne pathogens *(10, 35, 103)*. Shiga toxin–producing *E. coli* strains are widely known to be one of the most aciduric pathogens in fermented or acidic foods. Therefore, studies of LAB inhibition of *E. coli* are mainly focused on *E. coli* O157:H7.

Research concerning *E. coli* inhibition by LAB is more extensive than that on inhibition by other bacteria. Du et al. *(27)* selected LAB that could inhibit pathogenic *E. coli* and found three strains of *Lactobacillus acidophilus* (KLDS1.0901, KLDS1.0902, and KLDS1.1003) whose supernatants could inhibit *E. coli* ATCC 25922. Other investigations into control of *E. coli* O157:H7 proliferation yielded similar conclusions: LAB could effectively inhibit the growth of *E. coli* O157:H7 *(11, 29, 101)*. By combining different ratios of four LAB (*L. acidophilus, Lactobacillus rhamnosus, L. casei,* and *Lactobacillus plantarum*), Wang et al. *(104)* found that the best combination for inhibiting *E. coli* O157:H7 was a ratio of 3:1:3 of *L. rhamnosus*/*L. casei*/*L.*

TABLE 1. *Study results for inhibition of* Listeria monocytogenes *by LAB*

Study no.	*L. monocytogenes* strain	LAB	Substance	Method	Medium	Result	Reference
1	H4	*Lactobacillus delbrueckii* subsp. *lactis* NRRL B-5628	Cell-free supernatant	Well diffusion assay	Tryptic soy agar	0.7 cm[a]	*97*
	H8					0.8 cm	
	4B					0.7 cm	
	31C					0.7 cm	
2	4ab no. 10	*L. casei* 20012 pSB168	Suspension	Plate count	Skim milk	Obvious effect with increase in level of LAB	*72*
3	*L. monocytogenes*[b]	*L. curvatus* CWBI-B28mt	Suspension	Plate count	Fresh beef	No effect	*121*
		L. curvatus CWBI-B28wt				3 log CFU·g^{-1} [c]	
		Pediococcus acidilactici H				2.5 log CFU·g^{-1}	
		L. curvatus CWBI-B28wt + *P. acidilactici* H				4.5 log CFU·g^{-1}	
4	*L. monocytogenes*[d]	*Leuconostoc* ZLG3	Cell-free supernatant	Double agar diffusion method	*L. monocytogenes* culture medium	1.5 cm[a]	*125*
		Leuconostoc ZLG5				1.4 cm	
		Leuconostoc ZLG16				1.7 cm	
		Leuconostoc ZLG85				1.9 cm	
		Leuconostoc ZLG93				1.4 cm	
		Leuconostoc ZLG94				1.7 cm	
5	V7 (serotype 1)	*Streptococcus thermophilus*[e]	Suspension	Surface plated	Skim milk	100%[f]	*87*
	Ohio (serotype 4b)					>96%	

[a] Diameter of bacteriostatic ring.
[b] THT, Gembloux, Belgium.
[c] Decrease in level of *L. monocytogenes*.
[d] 4033 Laboratory, College of Food, Heilongjiang Bayi Agricultural University, Daqing, Heilongjiang, People's Republic of China.
[e] Marschall Division, Miles Laboratories, Madison, WI.
[f] Percent growth inhibition.

TABLE 2. *Study results for inhibition of* Staphylococcus aureus *by LAB*

Study no.	*S. aureus*		LAB	Substance	Method	Medium[a]	Result	Reference
1	Methicillin resistant	M2	*Lactobacillus salivarius* CNU1334, *L. fermentum* CNU1969	Bacterial suspension	Plate count	TSB	3 log CFU mL^{-1} [b]	*47*
		USA 300 JE2					2 log CFU mL^{-1}	
		USA 300 JE2					1 log CFU mL^{-1}	
	Methicillin susceptible	ATCC 25923					0	
		RN6390					4 log CFU mL^{-1}	
		8325-4					1 log CFU mL^{-1}	
2	196E		34 LAB cultures from stock culture collections	Bacterial suspension	Plate count	TSB	Complicated	*48*
	W-1							

[a] TSB, tryptic soy broth.
[b] Decrease in level of *S. aureus*.

TABLE 3. *Study results for inhibition of* Salmonella enterica *by LAB*

Study no.	*Salmonella* serovar	LAB	Substance	Method	Medium[a]	Result	Reference
1	Enteritidis Typhimurium	*Enterococcus faecium* 128, *E. faecium* 131, *Pediococcus parvulus* CE11_2	Bacterial suspension	Double agar diffusion method	MRS, TSA	0.7, 1.2, 1.0 cm[b] 1.15, 1.1, 0.975 cm	*114*
2	Typhi Ty2 Typhimurium LT2	35 native putative probiotic *Lactobacillus* strains of Indian gut origin, 4 standard probiotic strains	Cell-free supernatant	Well diffusion assay	BHI	Antibacterial activity ranges from high to low for various strains	*82*
3	Typhimurium SL1344	*L. rhamnosus* GG (ATCC 53103)	Cell-free supernatant	Plate count	MRS	8 log CFU mL^{-1} [c]	*50*
4	Typhimurium ATCC 14028	*L. plantarum, L. rhamnosus, L. bulgaricus, L. helveticus, L. casei, L. fermentum*	Bacterial suspension	Plate count	LB	*L. plantarum* generally more antagonistic to *Salmonella*	*118*

[a] MRS, de Man Rogosa Sharpe medium; TSA, tryptic soy agar; BHI, brain heart infusion; LB, Luria-Bertani medium.
[b] Diameter of bacteriostatic ring.
[c] Decrease in level of *Salmonella*.

TABLE 4. *Study results for inhibition of* Escherichia coli *by LAB*

Study no.	*E. coli*	LAB	Substance	Method	Medium[a]	Result	Reference
1	ATCC 25922	*Lactobacillus acidophilus* KLDS1.0901	Cell-free supernatant	Oxford cup	LB	2.21 cm[b]	*27*
		L. acidophilus KLDS1.0902				2.03 cm	
		L. acidophilus KLDS1.1003				2.16 cm	
2	O157:H7 strain 35150	*L. lactis* (from the Oklahoma State University Dairy Microbiology Laboratory)	Bacterial suspension	Plate count	MRS	3.5 log CFU mL^{-1} [c]	*11*
	O157:H7 strain 43890					3.0 log CFU mL^{-1}	
	O157:H7 strain 43894					2.6 log CFU mL^{-1}	
					Chicken meat	1.1 log CFU mL^{-1}	
3	O157:H7	*L. casei*	Culture supernatant	Turbidity survey, well diffusion assay	TSB	489 OD_{650},[d] 1.7 cm[b]	*29*
		L. acidophilus				492 OD_{650}, 1.6 cm	
		L. helveticus				495 OD_{650}, 1.35 cm	
		L. delbrueckii subsp. *bulgaricus*				485 OD_{650}, 1.4 cm	
4	O157:H7 strain UT 10	*L. plantarum* ATCC 8014	Bacterial suspension	Plate count	Beef loins	Higher level of *L. plantarum* resulted in earlier onset of *E. coli* O157:H7 inhibition	*101*
5	O157:H7	*L. acidophilus, L. rhamnosus, L. casei, L. plantarum, L. paracasei, Streptococcus thermophilus, L. brevis*	Bacterial suspension	Plate count, Oxford cup	YPD, MRS	Most effective combination for inhibition: *L. rhamnosus, L. casei, L. plantarum* (3:1:3)	*104*

[a] LB, Luria-Bertani medium, MRS, de Man Rogosa Sharpe medium; TSB, tryptic soy broth; YPD, yeast extract–peptone–dextrose medium.
[b] Diameter of bacteriostatic ring.
[c] Decrease in level of *E. coli*.
[d] OD value at 650 nm (OD_{650}) analyzed by turbidimetry method; the value for *E. coli* O157:H7 in pure culture is 2005.

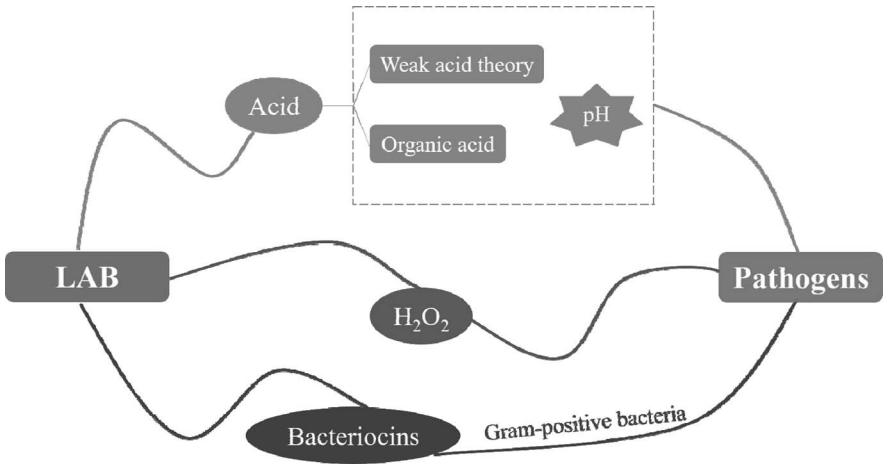

FIGURE 1. *Mechanism of LAB activity against pathogens.*

plantarum (Table 4). This combination of biological inhibitors was effective for addressing *E. coli* O157:H7 contamination.

Other pathogens. Studies concerning the use of LAB to inhibit other bacteria, especially foodborne pathogens, are not numerous, but in most studies positive results have been obtained in humans. Zhang et al. *(122)* found that four *Lactobacillus* strains (*Lactobacillus paracasei* subsp. *paracasei* M5-L, *L. rhamnosus* J10-L, *L. casei* Q8-L, and *L. rhamnosus* GG) isolated from traditional Chinese fermented foods in northwestern China could inhibit the growth of *Shigella sonnei*. This bacterium is an enteroinvasive pathogen that causes inflammatory destruction of the intestinal epithelium and leads to an acute rectocolitis with possibly lethal complications. *Klebsiella pneumonia, Bacillus cereus, Shigella flexneri (90), Staphylococcus epidermidis (24),* and *Candida albicans (117)* also can be inhibited by LAB to various degrees (Table 5). Thus, LAB have potential uses as probiotics to prevent and treat infections caused by foodborne pathogens.

MECHANISMS OF THE ANTAGONISTIC ACTION OF LAB

The mechanisms by which LAB affect foodborne pathogens are not completely understood. Although opinions are diverse, most researchers agree that the bacteriostatic phenomenon is caused by a few factors jointly. The main possible contributors to the inhibitory effects of LAB are shown in Figure 1.

Acid production is thought to be the most important mechanism by which LAB inhibit pathogens; bacteria are gradually inactivated as the pH gets lower *(37, 108)*. The weak acid theory also may be important. Weak acids are lipophilic when not dissociated; thus, they can enter a bacterial cell through the plasma membrane and decompose into ions in a high pH environment, causing acidification of the cytoplasm. Acidification can alter the cell metabolism by damaging enzymes, inhibiting protein synthesis, destroying genetic material, interrupting nutrient absorption, and damaging the substructure and function of cell wall and membranes *(54)*. Stratford et al. *(95)* confirmed acetic acid inhibition of *Saccharomyces cerevisiae* in accordance with this theory. Organic acids have multiple inhibitory activities, including energy competition *(21),* intracellular anion accumulation (which increases intracellular osmotic pressure) *(59, 81),* membrane effects *(5, 41),* inhibition of biomacromolecule synthesis *(76),* induction of host cell to produce antimicrobial peptides *(12),* and intracellular pH effects. Zhang et al. *(119)* proposed that the aggregation of acid ions in the bacterial intracellular space is an important determinant of the antibacterial action of organic acids.

Tharrington and Sorrells *(97)* treated *Lactobacillus delbrueckii* culture filtrate with heat and catalase and found that heat did not significantly affect the antimicrobial activity, but catalase treatment decreased inhibition. This experiment revealed that hydrogen peroxide (known to be produced by LAB *(77)*) was one of the major factors in inhibition of pathogen growth.

Bacteriocins also are important antimicrobial compounds. Bacteriocins are polypeptides or precursor polypeptides with antibacterial activity that are produced by some bacteria during ribosomal synthesis. An ingenious control experiment in which a mutated strain of *Lactobacillus curvatus* (CWBI-B28mt) that did not produce bacteriocin was used as the negative control revealed that bacteriocins may be antimicrobial factors *(121)*. Perales-Adan et al. *(75)* found two kinds of bacteriocins, the enterocin AS-48 *(17, 36)* and the lantibiotic nisin, that had strong antibacterial effects and were more efficacious when combined. However, bacteriocins are mostly effective against gram-positive bacteria.

The differences in the antimicrobial mechanisms reported by various researchers may be attributed to the diversity in gene expression or molecular structures of tested bacterial strains, which result in differences in acid tolerance, hydrogen peroxide tolerance, and sensitivity to bacteriocins.

COMPETITIVE GROWTH MODEL OF LAB AND PATHOGENS

Jameson effect model. In 1962, Jameson *(44)* first proposed that when two intestinal organisms were grown together in a liquid medium each microbe would proliferate rapidly at the outset, as if they were grown alone, and then both would stop growing when one microbe reached the

TABLE 5. *Study results for inhibition of other pathogens by LAB*

Study no.	Pathogen	LAB	Substance	Method	Medium[a]	Result	Reference
1	*Escherichia coli* ATCC 25922 *Salmonella* Typhimurium ATCC 14028 *Shigella sonnei* ATCC 25931	*Lactobacillus paracasei* M5-L, *L. rhamnosus* J10-L, *L. casei* Q8-L, *L. rhamnosus* ATCC 53103	Cell-free supernatant	Well diffusion assay	TSA	+, +, ++, ++[b] ++, +, +, ++ ++, ++, +++, ++	*122*
2	*Staphylococcus aureus, Listeria monocytogenes, E. coli, Klebsiella pneumoniae* *Bacillus cereus, Salmonella* Typhi, *Shigella flexneri* *Pseudomonas aeruginosa, Proteus mirabilis* *Streptococcus mutans*	31 strains (20 from curds and 11 from human milk) of five species: *L. casei, L. delbrueckii, L. fermentum, L. plantarum, L. pentosus*	Cell-free supernatant	Well diffusion assay	MHA	No inhibition Moderate inhibition by majority of supernatants Weak inhibition Some curd isolates were antagonistic	*90*
3	*S. aureus* ATCC 12600, *S. epidermidis* 575/08, *S. xylosus* 35/37, *Streptococcus uberis* ATCC 700407, *S. agalactiae* ATCC 27956, *E. coli* DSM 4230	367 wild isolates, 2 reference strains (*Lactococcus lactis* subsp. *lactis* ATCC 11454, *Lactobacillus rhamnosus* ATCC 7469), 6 combinations of wild and reference strains	Cell-free supernatant	Well diffusion assay	MHA	170 wild isolates inhibited *S. uberis,* 78 inhibited *S. epidermidis,* 37 inhibited *S. aureus,* 36 inhibited *S. xylosus,* 14 inhibited *E. coli,* 13 inhibited *S. agalactiae*; 2 combinations inhibited all six pathogens	*24*
4	*E. coli* *S. aureus* *Candida albicans*	*L. acidophilus, L. casei, L. bulgaricus* (1), *L. bulgaricus* (2)	Cell-free supernatant	Agar diffusion test	LB	2.1, 1.9, 1.9, 2.9 cm[c] 2.1, 1.6, 1.6, 1.8 cm 1.2, 1.4, 1.1, 1.1 cm	*117*

[a] TSA, tryptic soy agar; MHA, Mueller-Hinton agar; LB, Luria-Bertani medium.
[b] Diameter of inhibition zone observed with growing cells: +, 1 mm; ++, 2 mm; +++, 2 to 5 mm.
[c] Diameter of bacteriostatic ring (cm).

maximum level. This phenomenon was eventually introduced to the field of predictive microbiology by Ross et al. *(83)* in 2000 and named the Jameson effect. Using an assumption based on this effect and some findings published during the 1990s *(13, 16),* Cornu *(19)* developed a model assuming the simultaneous deceleration of the growth of both microorganisms in coculture.

As summarized by Cornu et al. *(20),* a generic primary Jameson effect model can be expressed as follows:

$$\frac{1}{N(t)}\frac{dN(t)}{dt} = \frac{d\{\ln[N(t)]\}}{d(t)} = \mu_{max} \cdot \alpha(t) \cdot f(t) \quad (1)$$

in which $N(t)$ is the population of tested microorganism, μ_{max} is the maximum growth rate, and $\alpha(t)$ and $f(t)$ are the adjustment function and inhibition function, respectively.

In other primary growth models, $\alpha(t)$ and $f(t)$ are written in different ways. For the Baranyi and Roberts model *(9),*

$$\alpha(t) = \frac{q(t)}{1+q(t)} \text{ with } \frac{1}{q(t)}\frac{dq(t)}{dt} = \mu_{max} \text{ and}$$
$$q(0) = q_0 = \frac{1}{e^{\mu_{max}\text{lag}} - 1} \quad (2)$$

where $q(t)$ is the physiological state of the cells and lag is the lag time and

$$f(t) = 1 - \frac{N(t)}{N_{max}} \quad (3)$$

where N_{max} is the maximal population density. For the three-phase linear model *(14),*

$$\alpha(t) = \begin{cases} 0 \text{ if } t < \text{lag} \\ 1 \text{ if } t \geq \text{lag} \end{cases} \quad (4)$$

$$f(t) = \begin{cases} 1 \text{ if } t < t_{max} \\ 0 \text{ if } t \geq t_{max} \end{cases} \text{ with } N(t_{max}) = N_{max} \quad (5)$$

where t_{max} is the time at which $N(t)$ reaches N_{max}.

Many modified versions of $f(t)$ have been proposed for various competitive organisms *(33, 52, 60)*. Combined with equation 1, all versions can describe the growth of competing bacteria in the same environment.

Lotka-Volterra competition model. Many researches have made use of the Lotka-Volterra competition model to explain the growth of cocultured bacteria *(31, 34, 74, 102)*. A useful model for mixed cultures of microorganisms was described *(7)*:

$$\begin{cases} \frac{dN_A}{dt} = r_A \frac{N_A}{K_A}(K_A - N_A - \alpha_{AB}N_B) \\ \frac{dN_B}{dt} = r_B \frac{N_B}{K_B}(K_B - N_B - \alpha_{BA}N_A) \end{cases} \quad (6)$$

where r_A and r_B and N_A and N_B represent the intrinsic growth rate and number of species A and species B, respectively; K is the saturation level for each bacterium; and α_{AB} is a coefficient of interaction effects of species B on species A and vice versa.

Because taking all dependencies into account is unpractical and meaningless, Dens et al. *(22)* modified the Lotka-Volterra model by considering the valuable and important factors:

$$\begin{cases} \frac{dN_A}{dt} = \mu_{max_A} \frac{q_A}{1+q_A} \frac{N_A}{N_{max_A}}(N_{max_A} - N_A - \alpha_{AB}N_B) \\ \frac{dN_B}{dt} = \mu_{max_B} \frac{q_B}{1+q_B} \frac{N_B}{N_{max_B}}(N_{max_B} - N_B - \alpha_{BA}N_A) \\ \frac{dq_A}{dt} = \mu_{max_A} q_A \\ \frac{dq_B}{dt} = \mu_{max_B} q_B \end{cases} \quad (7)$$

where q_A and q_B are variables that represent the physiological states of the two kind of cells, as the variable in the Baranyi and Roberts model (equation 2). The model combined the advantages of the Lotka-Volterra model with features of Baranyi and Roberts model, which can describe the three growth stages (lag, exponential, and stationary) of two competitive microorganisms.

Ye et al. *(115)* described a model for the interval $[t_i, t_{i+1}]$ to calculate the least-square solution more conveniently:

$$\begin{cases} \ln N_A(t_{i+1}) - \ln N_A(t_i) = \mu_{max_A} \times \frac{q_A}{1+q_A} \times (t_{i+1} - t_i) \\ \qquad - \sum_{t_i}^{t_{i+1}} N_A(t)dt - \alpha_{AB} \\ \qquad \times \sum_{t_i}^{t_{i+1}} N_B(t)dt \\ \ln N_B(t_{i+1}) - \ln N_B(t_i) = \mu_{max_B} \times \frac{q_B}{1+q_B} \times (t_{i+1} - t_i) \\ \qquad - \sum_{t_i}^{t_{i+1}} N_B(t)dt - \alpha_{BA} \\ \qquad \times \sum_{t_i}^{t_{i+1}} N_A(t)dt \end{cases} \quad (8)$$

This modified model may be not able to precisely describe the growth state of bacteria under a competitive condition, but its idea of parameter modification and model optimization is worth thinking about and may provide a direction for future research to improve the model.

APPLICATION OF THE INHIBITORY ACTIVITY OF LAB TO PATHOGENS

With continuous improvements in the quality of human life, food safety is garnering more attention. The emphasis has been on both inactivation of foodborne pathogens and on keeping microbial levels in food below regulatory standards in way that is beneficial to human health. In 1997, Jay *(45)* proposed that fresh foods with too few microorganisms may not be the safest. Jay suggested that an appropriate background microbiota in food products is important for outcompeting pathogenic microbes and keeping food safe. LAB have become popular in recent years because of their antibacterial properties and ability to inhibit pathogen growth and increase the nutritional value of food. The main applications for LAB in food are preservation of dairy products, raw meat and its products, fresh fruits and vegetables, and aquatic products *(91)*.

LAB fermentation is one of the oldest and most effective ways to prevent vegetable spoilage and deterioration and thus plays an important role in food storage. Wouters et al. *(112)* found that *L. plantarum* IMDO 788 was a better starter culture for fermentation of vegetables (carrot, cauliflower, and green tomato) than was the endogenous LAB community. Zhang et al. *(120)* studied the microbiota of jiangshui, a traditional Chinese fermented vegetable food, and found a unique bacterial community. LAB of many other fermented vegetable foods have been studied, e.g., kimchi *(8),* pickled mustard tuber *(113),* Chinese northeast sauerkraut *(18, 64),* and fermented pepper *(106)*. LAB also may play a role in preservation of fresh cut

fruits and vegetables, such as apples, pears, and lettuce *(42, 100)*.

The use of LAB for reducing the microbial risks associated with various foods is rare in food production facilities; most of the research has been theoretical studies conducted in laboratories. As a milk product produced by LAB fermentation, cheese is one of the best experimental media. Various types of cheeses have been studied to determine the antibiotic properties of the endogenous LAB against *L. monocytogenes*. This pathogen can survive during the manufacture and storage stages of Feta cheese *(73),* cottage cheese *(85),* and Mexican Manchego and Chihuahua cheese *(94)*. Ahmadzadeh Nia and Hanifian *(3)* found that the addition of *L. plantarum* is effective for control the amount of *L. monocytogenes* in ultrafiltered white cheese. Langa et al. *(51)* found that reuterin-producing *Lactobacillus reuteri* INIA P572 had a powerful antimicrobial effect on *L. monocytogenes* and *E. coli* O157:H7. Ho et al. *(40)* tested nondairy LAB strains and found that *Lactobacillus lactis* strains from herbs, fruits, and vegetables were effective as biopreservatives in cheese manufacturing. The behavior of pathogens in cheese is quite variable. *B. cereus* can tolerate the low pH conditions of ultrafiltered Feta cheese until the end of its shelf life *(67)*. *Mycobacterium avium* subsp. *paratuberculosis* levels remained stable during the storage period for ultrafiltered white cheese *(38)*. In contrast, *S. aureus* was controlled below the regulatory limit in Iranian ultrafiltered white cheese *(65)*. *Yersinia enterocolitica* counts diminished during the storage period in ultrafiltered white cheese despite a significant increase in the population after incubation *(2)*. Therefore, the inhibitory properties of LAB against pathogens in cheese can differ dramatically.

LAB have been used as antimicrobial agents in foods other than cheese *Lactobacillus* can be an excellent preserver of fresh meat, inhibiting the growth of *L. monocytogenes, Salmonella* Typhimurium, and *E. coli* O157:H7 in beef *(70, 89),* controlling the levels of *Salmonella* Typhimurium and *E. coli* O157:H7 in pork *(89)* and extending its shelf life *(68),* and reducing the levels of *L. monocytogenes* and *Salmonella* Enteritidis in chicken *(56)*. Slima et al. *(92)* found that *L. plantarum* TN8 decreased the level of *Salmonella enterica* and *L. monocytogenes* and maintained lipid oxidation in beef sausages, which means that *Lactobacillus* can be a potential biopreservative in manufactured meat. The addition of LAB to cold-smoked wild salmon *(96)* and mackerel mince *(116)* prevented proliferation of pathogens in these fish products.

Although LAB can have many positive effects in foods, inhibition of pathogens in foods may also result in food spoilage. Hence, appropriate ways to utilize LAB as effective bacteriostatic agents in food needs more research.

PROSPECT OF THE RESEARCH

The use of LAB suspensions and cell-free supernatants as antibacterial agents is still a popular and underevaluated area of research; LAB have unique advantages for application in industrial food production. Thus, identification of the bacteriostatic compounds produced by LAB is particularly important. The mechanisms of the inhibitory action and identification of the most effective LAB species and strains for each pathogen in various food also must be determined to allow translation of LAB protocols from the laboratory to industry.

The use of LAB is a potentially feasible approach to problems associated the emergence of antibiotic-resistant bacteria, which have caused widespread concern in academia and in human nutrition. Although very little is known about the antibiotic resistance of environmental bacteria *(6),* numerous investigations are in progress to determine the mechanisms of resistance. Antibiotic resistance occurs through intrinsic resistance of the bacteria, spontaneous gene mutations, or horizontal gene transfer *(26)*. In the first two cases, LAB may be an ideal tool against resistant microorganisms, inhibiting the "stubborn" pathogens and reducing the use of antibiotics, which should be carefully controlled *(53)* to avoid the potential threats of antimicrobial resistance and selective pressure among pathogenic bacteria *(63, 88, 98)*. The application of LAB in the field of horizontal gene transfer *(1, 79, 86, 99, 110)* awaits further study. The challenge of this situation is complicated. Resistant pathogens may transfer resistance genes to LAB, and LAB carrying resistance genes may pass these genes to other bacteria in the human body.

The antimicrobial effects of LAB on pathogens has potentially wide application in such fields as the food industry, medical treatment, and public hygiene. More research is needed on the conditions under which LAB inhibit pathogens in food and on the mechanisms of this antimicrobial action.

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