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Review

ANTIMICROBIAL ACTIVITY OF *LACTOBACILLUS PLANTARUM* AGAINST PATHOGENIC AND FOOD SPOILAGE MICROORGANISMS: A REVIEW

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Summary

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One of the most important properties of probiotic bacteria is their antimicrobial activity against many species of microorganisms which could be useful to prevent food spoilage caused by certain sensitive bacteria and fungi as well as to control the speed of propagation of potentially pathogenic bacteria by probiotic application. *Lactobacillus plantarum* is considered one of the probiotic bacteria with broadest spectrum of antibacterial activity which makes it useful in veterinary, human medicine and food industry. According to a number of studies *Lactobacillus plantarum* exerts inhibitory activity against many Gram-positive and Gram-negative bacteria – *Escherichia coli* (including *E. coli* 0157:H7), *Pseudomonas aeruginosa*, *Helicobacter pylori*, *Yersinia enterocolitica*, *Campylobacter jejuni*, *Listeria monocytogenes*, *Staphylococcus aureus*, *Klebsiella*, *Salmonella*, *Shigella*, *Bacillus*, *Clostridium*, *Enterococcus*, *Lactobacillus spp.*, etc. as well as a number of moulds and yeasts – *Aspergillus*, *Fusarium*, *Mucor*, *Candida* spp., etc. The main antibacterial compounds of *Lactobacillus plantarum* are the bacteriocins and organic acids whereas the antifungal compounds are the organic acids, hydroxy fatty acids and cyclic dipeptides. Because of the high antifungal activity of some *L. plantarum* strains against food spoilage microorganisms they can be used as effective biopreservatives in food industry. Also, some *L. plantarum* strains could be applied as supporting therapeutic agents in treatment of infections caused by the corresponding susceptible microorganisms.

Key words: antimicrobial activity, *Lactobacillus plantarum*, food spoilage microorganisms, pathogens

INTRODUCTION

Spoilage of food products by bacteria and fungi is a worldwide problem. They can cause extensive damage of the food such as unpleasant smell, taste or appearance as well as formation of harmful substances for the consumer's health. Also, another

important aspect of food contamination by microorganisms is the presence of potentially pathogenic species, which pose a great risk for the human and animal health (Broberg *et al.*, 2007). One of the most important properties of probiotic bacteria is their antimicrobial activity against many species of microorganisms which could be useful in order to avoid the constant application of antibiotics and to control the speed of propagation of potentially pathogenic intestinal bacteria (Arias *et al.*, 2013).

Lactobacillus plantarum (*L. plantarum*) is a member of lactic acid bacteria (LAB). It is an important species taking part in the fermentation of many plant products (silage, sauerkraut, brined olives, pickles), sourdough, cheeses, fermented sausages and stockfish (Cebeci & Gürakan, 2003). It belongs to the probiotic *Lactobacillus* species inhabiting the human digestive system and producing bacteriocins, exopolysaccharides, extracellular proteins and lipoteichoic acids. They improve the health and physiology of the host by interacting with epithelial cells and enhancing the host immune system (Arasu *et al.*, 2016). Recently *L. plantarum* has been applied in human medicine for treatment of chronic inflammation associated with various diseases including cancer, Parkinson's disease, Alzheimer's disease and cardiovascular diseases (Woo *et al.*, 2014). Kurhan & Çakir (2016) reported that *L. plantarum* has DNA-bioprotective effect reducing the aflatoxin B_1 genotoxic effect on colon adenocarcinoma (Caco-2) cells. Comparative studies between different probiotics showed that *L. plantarum* strains demonstrated the broadest spectrum of antimicrobial activity among the probiotic bacteria examined (Dembélé *et al.*, 1998; Wang *et al.*, 2010; Ren *et al.*, 2014; Dubourg *et al.*, 2015; Davoodabadi *et al.*, 2015).

Considering the increasing importance of the LAB as antibiotics alternative, the knowledge of the antimicrobial activity of the main LAB species and *L. plantarum* in particular is of especially high significance. The antimicrobial activity of *L. plantarum* can show if its products can be helpful in the treatment of a particular infection or if they can prevent the development of undesirable microbiota in food products. In that way the supplementation of *L. plantarum* products could be made on the basis of the antimicrobial activity of the particular *L. plantarum* strain.

ANTIMICROBIAL COMPOUNDS PRODUCED BY *L. PLANTARUM*

Bacteriocins

Bacteriocins are ribosomally synthesised antimicrobial peptides produced by various bacteria, including LAB. Some of them have great potential in food preservation and can reduce or eliminate the need for addition of chemical preservatives or the intensity of processing the food and in that way can satisfy the demand for high-quality foods (Perez *et al.*, 2014). To guarantee bacteriocin effectiveness when supplemented to the food it should be tested against specific target microorganisms in the type of food for which they are intended to be used. Most of the bacteriocins kill the susceptible bacteria by inducing permeabilisation and pore formation on the cytoplasmic membrane or by interactions with essential enzymes (Wen *et al.*, 2016). Because bacteriocins are degraded by the proteolytic enzymes of the gastrointestinal tract and seem to be non-toxic and non-antigenic to animals and humans they can be used to improve the safety and shelf-life of many food products (Amenu, 2013). When selecting bacteriocins for food application

the following criteria should be considered: the bacteriocin-producing strain should be generally recognised as safe; the bacteriocin should: 1) have a broad spectrum of inhibition against a variety of food-borne pathogens or specificity against a particular pathogen specific for given food; 2) have high degree of heat stability; 3) lead to beneficial effects in the product such as improved safety and quality; 4) have a high specific activity (O'Sullivan *et al.*, 2002).

Organic acids

L. plantarum is facultative heterofermentative species that ferment carbohydrates to produce lactic acid and ethanol or acetic acid. Organic acid lowers the local pH and therefore inhibits the growth of bacteria, sensitive to acidic conditions. The low pH makes organic acids liposoluble, allowing them to break through the cell membrane and reach the cytoplasm of target microorganisms (Haller *et al.*, 2001). However, the microorganisms differ considerably in their sensitivity to lactic acid. At pH 5.0 lactic acid exert inhibitory activity towards spore- forming bacteria but is ineffective against yeast and moulds (Amenu, 2013). Acetic and propionic acids produced by *L. plantarum* strains through heterofermentative pathways, may interact with cell membranes and cause intracellular acidification and protein denaturation (Urga *et al.*, 1992). They have higher antimicrobial activity than lactic acid due to their higher pKa values (lactic acid 3.08, acetic acid 4.75, and propionic acid 4.87), and higher percent of undissociated acids than lactic acid at a given pH (Earnshaw, 1992).

Hydroxy fatty acids

There are several studies indicating that 3-hydroxy fatty acids have antifungal activity which is due to detergent-like properties of the compounds that alter cellular membrane structure in the target organisms (Sjögren *et al.*, 2003). According to studies on LAB-produced antimicrobial fatty acids, they have a broad spectrum of antifungal activity (Sjögren *et al.*, 2003; Dalié *et al.*, 2010).

Hydrogen peroxide

Hydrogen peroxide is produced by *L. plantarum* and the other LAB in the presence of oxygen as a result of the action of flavoprotein oxidases or NADH peroxidase. The antimicrobial activity of hydrogen peroxide could be the result of the oxidation of sulfhydryl groups causing denaturation of a number of enzymes, and from the peroxidation of membrane lipids leading to increased membrane permeability (Amenu, 2013). Hydrogen peroxide can be a precursor for the production of bactericidal free radicals such as superoxide (O_2^-) and hydroxyl (OH^-) radicals which can damage DNA (Byczkowski & Gessner, 1988). According to Gerez *et al.* (2013) hydrogen peroxide does not exert any antifungal activity.

Carbon dioxide

Carbon dioxide is mainly produced by heterofermentative LAB. Because *L. plantarum* is facultative heterofermentative species, depending on the carbon source it can switch between using heterofermentative and homofermentative ways of metabolism (Kleerebezem *et al.*, 2003). The precise mechanism of the antimicrobial action of carbon dioxide is still poorly understood. However, carbon dioxide may play a role in creating an anaerobic environment, which inhibits enzymatic decarboxylations, and the accumulation of carbon dioxide in the membrane lipid bilayer is a possible cause for permeability dysfunction (Eklund, 1984).

ANTIMICROBIAL ACTIVITY OF *L. PLANTARUM* AGAINST PATHOGENIC AND FOOD SPOILAGE MICROORGANISMS

Antibacterial activity of L. plantarum

According to the experimental data *L. plantarum* is active against many Gram-negative pathogens and food spoilage microorganisms – *Escherichia coli* (including enteropathogenic, enterotoxigaenic, enteroinvasive, multidrug-resistant enteroaggregative *E. coli* and *E. coli* 0157:H7), *Pseudomonas aeruginosa*, *Yersinia enterocolitica*, *Campylobacter jejuni*, *Helicobacter pylori*, *Klebsiella*, *Salmonella*, *Shigella* spp., etc. (Table 1). Also *L. plantarum* exerts inhibitory activity against a variety of potentially harmful Gram-positive bacteria – *Listeria monocytogenes*, *Staphylococcus aureus* and some members of the genera *Bacillus*, *Clostridium*, *Enterococcus*, *Lactobacillus*, etc. (Table 2). It is important to emphasise that the antimicrobial activity of *L. plantarum* (and the other LAB) is strain specific, i.e. only some strains of *L. plantarum* are inhibitory toward specific strains of the microbial species (Denev *et al.*, 2015). There are three mechanisms that could explain the antimicrobial activity of LAB and *L. plantarum* in particular: the production of bacteriocins; the yield of organic acids and other inhibitory substances such as ethanol, carbon dioxide and hydrogen peroxide; and the competition for nutrients (Magnusson *et al.*, 2003).

L. plantarum strains produce a broad range of bacteriocins such as ST28MS, ST26MS, bacST202Ch, bacST216Ch, ST71KS, AMA-K, plantaricin B, D, G, K, K25, S, BN, UG1, S, T, C19, CTC 305, CTC 306, 35d, Q7, MG, 163, ASM1, EF, JK, N, NC8, ZJ008, etc. (Enan *et al.*, 1996; Todorov & Dicks, 2005; Todorov *et al.*, 2007; 2010; Hata *et al.*, 2010; Gong *et al.*, 2010; Martinez *et al.*, 2013; Buntin & Hongpattarakere, 2014; Zhu *et al.*, 2014; Jiang *et al.*, 2016; Liu *et al.*, 2016; Wen *et al.*, 2016). Different *L. plantarum* bacteriocins have bactericidal mode of action and diverse antimicrobial spectrum of activity. They usually have narrow spectrum of activity against closely related Gram-positive bacteria from *Lactobacillaceae*, whereas producer cells are immune to their own bacteriocins (Abo-Amer, 2013). It is well established that Gram-negative bacteria are intrinsically resistant to bacteriocins produced by LAB due to the presence of external membrane, which constitutes a physical barrier to the passage and binding of bacteriocins (Pehrson *et al.*, 2015). However, it has been reported that the destabilisation of the outer membrane can make Gram-negative bacteria susceptible to these bacteriocins. It is found that lactic acid acts as a permeabiliser of the outer membrane of Gram-negative bacteria, thus increasing their susceptibility to antimicrobials (including bacteriocins), allowing their molecules to penetrate the bacteria (Alakomi *et al.*, 2000).

There are also some bacteriocins having a broad range of inhibition against Gram-positive and Gram-negative bacteria including food-borne pathogens such as *Listeria monocytogenes*, *Escherichia coli*, *Staphylococcus aureus*, *Clostridium perfringens*, *Pseudomonas spp.* etc., and antimicrobial resistance is not likely to be induced after their application (Gong *et al.*, 2010; Todorov *et al.*, 2010). Because the bacteriocins produced by certain strains of *L. plantarum* sometimes exert antibacterial activity against a large number of Gram-positive and Gram-negative spoilage and pathogenic bacteria, the respective *L. plantarum* strains are suitable

Table 1. Antibacterial activity of *Lactobacillus plantarum* strains against Gram-negative bacteria

Spectrum of *L. plantarum* activity	References
Acinetobacter baumannii	Todorov & Dicks, 2005
Bacteroides thetaiotaomicron	Dubourg *et al.*, 2015
Campylobacter jejuni	Patel *et al.*, 2013
Citrobacter freundii	Dal Bello *et al.*, 2007
Enterobacter aerogenes	Tambekar & Bhutada, 2009
Enterobacter cloacae	Dubourg *et al.*, 2015
Erwinia persicina	Jiang *et al.*, 2016
Escherichia coli	Todorov & Dicks, 2005; Dal Bello *et al.*, 2007; Todorov *et al.*, 2007; Tambekar & Bhutada, 2009; Gong *et al.*, 2010; Wang *et al.*, 2010; Todorov *et al.*, 2010; Patel *et al.*, 2013; Buntin & Hongpattarakere, 2014; Peres *et al.*, 2014; Ren *et al.*, 2014; Zhu *et al.*, 2014; Davoodabadi *et al.*, 2015; Dubourg *et al.*, 2015; Pehrson *et al.*, 2015; Venkadesan & Sumathi, 2015; Liu *et al.*, 2016; Aoudia *et al.*, 2016; Kumar *et al.*, 2016; Wen *et al.*, 2016
Helicobacter pylori	Sunanliganon *et al.*, 2012
Klebsiella pneumoniae	Todorov *et al.*, 2007; Tambekar & Bhutada, 2009; Todorov *et al.*, 2010; Omemu & Faniran, 2011; Ren *et al.*, 2014; Khan & Kang, 2016
Pseudomonas spp.	Todorov *et al.*, 2010
P. aeruginosa	Todorov & Dicks, 2005; Rodríguez *et al.*, 2012; Peres *et al.*, 2014; Todorov *et al.*, 2014; Zhu *et al.*, 2014; Dubourg *et al.*, 2015; Khan & Kang, 2016; Liu *et al.*, 2016; Wen *et al.*, 2016
P. fluorescens	Gong *et al.*, 2010
Proteus vulgaris	Dal Bello *et al.*, 2007; Tambekar & Bhutada, 2009
P. mirabilis	Omemu & Faniran, 2011; Dubourg *et al.*, 2015
Salmonella enterica subsp. *arizonae*	Jiang *et al.*, 2016
S. enterica subsp. *enterica*	Wang *et al.*, 2010; Rodríguez *et al.*, 2012; Jiang *et al.*, 2016
S. enterica subsp. *enterica ser.* Enteritidis	Davoodabadi *et al.*, 2015; Pehrson *et al.*, 2015; Aoudia *et al.*, 2016
S. Paratyphi	Buntin & Hongpattarakere, 2014; Jiang *et al.*, 2016
S. Typhi	Tambekar & Bhutada, 2009; Venkadesan & Sumathi, 2015
S. Typhimurium	Gong *et al.*, 2010; Patel *et al.*, 2013; Buntin & Hongpattarakere, 2014; Hongpattarakere & Uraipan, 2014; Peres *et al.*, 2014; Ren *et al.*, 2014; Jiang *et al.*, 2016; Liu *et al.*, 2016
Shigella spp.	Venkadesan & Sumathi, 2015
S. flexneri	Tambekar & Bhutada, 2009; Zhu *et al.*, 2014; Davoodabadi *et al.*, 2015; Liu *et al.*, 2016
S. sonnei	Buntin & Hongpattarakere, 2014; Davoodabadi *et al.*, 2015; Pehrson *et al.*, 2015; Liu *et al.*, 2016
Vibrio parahaemolyticus	Zhu *et al.*, 2014; Jiang *et al.*, 2016
Yersinia enterocolitica	Patel *et al.*, 2013; Davoodabadi *et al.*, 2015

Table 2. Antibacterial activity of *Lactobacillus plantarum* strains against Gram-positive bacteria

Spectrum of *L. plantarum* activity	References
Bacillus cereus	Enan *et al.*, 1996; Elegado *et al.*, 2004; Gong *et al.*, 2010; Wang *et al.*, 2010; Omemu & Faniran, 2011; Ren *et al.*, 2014; Wen *et al.*, 2016; Zhang *et al.*, 2016
B. subtilis	Elegado *et al.*, 2004; Dal Bello *et al.*, 2007; Valerio *et al.*, 2008; Gong *et al.*, 2010; Peres *et al.*, 2014; Zhu *et al.*, 2014
Clostridium difficile	Schoster *et al.*, 2013; Dubourg *et al.*, 2015
C. perfringens	Enan *et al.*, 1996; Gong *et al.*, 2010; Schoster *et al.*, 2013
Enterococcus avium	Inglin *et al.*, 2015
E. casseliflavus	Inglin *et al.*, 2015
E. durans	Inglin *et al.*, 2015
E. faecalis	Elegado *et al.*, 2004; Todorov & Dicks, 2005; Dal Bello *et al.*, 2007; Todorov *et al.*, 2007; Hata *et al.*, 2010; Patel *et al.*, 2013; Peres *et al.*, 2014; Todorov *et al.*, 2014; Dubourg *et al.*, 2015; Inglin *et al.*, 2015
E. mundtii	Todorov *et al.*, 2007
Lactobacillus alimentarius	Enan *et al.*, 1996
L. casei	Enan *et al.*, 1996; Elegado *et al.*, 2004
L. curvatus	Enan *et al.*, 1996; Todorov *et al.*, 2007; Hata *et al.*, 2010; Todorov *et al.*, 2010; Inglin *et al.*, 2015
L. delbrueckii	Elegado *et al.*, 2004; Todorov *et al.*, 2010
L. fermentum	Enan *et al.*, 1996; Todorov *et al.*, 2010
L. helveticus	Enan *et al.*, 1996
L. johnsonii	Todorov *et al.*, 2010
L. lindneri	Hata *et al.*, 2010
L. paraplantarum	Todorov *et al.*, 2010
L. pentosus	Enan *et al.*, 1996; Hata *et al.*, 2010; Todorov *et al.*, 2010
L. plantarum	Hata *et al.*, 2010; Elegado *et al.*, 2004
L. rhamnosus	Todorov *et al.*, 2010
L. sakei	Todorov & Dicks, 2005; Todorov *et al.*, 2007
L. salivarius	Todorov *et al.*, 2007; Todorov *et al.*, 2010
Lactococcus lactis	Enan *et al.*, 1996; Todorov *et al.*, 2007; Todorov *et al.*, 2010
Leuconostoc mesenteroides	Elegado *et al.*, 2004
Listeria spp.	Dembélé *et al.*, 1998
L. monocytogenes	Enan *et al.*, 1996; Elegado *et al.*, 2004; Todorov *et al.*, 2007; Gong *et al.*, 2010; Nielsen *et al.*, 2010; Todorov *et al.*, 2010;Wang *et al.*, 2010; Rodríguez *et al.*, 2012; Martinez *et al.*, 2013; Buntin & Hongpattarakere, 2014; Peres *et al.*, 2014; Todorov *et al.*, 2014; Zhu *et al.*, 2014; Asurmendi *et al.*, 2015; Dubourg *et al.*, 2015; Engelhardt *et al.*, 2015; Inglin *et al.*, 2015; Venkadesan & Sumathi, 2015; Aoudia *et al.*, 2016; Liu *et al.*, 2016; Wen *et al.*, 2016
L. ivanovii	Todorov *et al.*, 2010; Inglin *et al.*, 2015
L. grayi	Elegado *et al.*, 2004

Table 2 (cont'd). Antibacterial activity of *Lactobacillus plantarum* strains against Gram-positive bacteria

Spectrum of *L. plantarum* activity	References
Pediococcus sp.	Elegado *et al.*, 2004
P. acidilactici	Elegado *et al.*, 2004
P. pentosaceus	Elegado *et al.*, 2004
Staphylococcus aureus	Dembélé *et al.*, 1998; Todorov & Dicks, 2005; Dal Bello *et al.*, 2007; Gong *et al.*, 2010; Todorov *et al.*, 2010; Wang *et al.*, 2010; Omemu & Faniran, 2011; Rodríguez *et al.*, 2012; Patel *et al.*, 2013; Buntin & Hongpattarakere, 2014; Peres *et al.*, 2014; Ren *et al.*, 2014; Zhu *et al.*, 2014; Dubourg *et al.*, 2015; Venkadesan & Sumathi, 2015; Liu *et al.*, 2016
S. epidermidis	Zhu *et al.*, 2014; Jiang *et al.*, 2016
Streptococcus spp.	Todorov *et al.*, 2007; Todorov *et al.*, 2010

for use as starter cultures in the fermentation of different products and to prolong shelf life (Todorov *et al.*, 2010).

The antibacterial effect of *L. plantarum*-produced cyclic dipeptides could be explained by the hydrophobic nature of the compounds, which could interfere with outer membrane (Gram-negative) and cytoplasma membrane (Gram-positive) function (Milne *et al.*, 1998; Rhee, 2004). In previous studies, cyclic dipeptides showed a broad spectrum of antibacterial activity (Milne *et al.*, 1998; Ström *et al.*, 2002; Rhee, 2004).

Regarding the inhibition effect caused by LAB and *L. plantarum* in particular, it is considered that the LAB-produced organic acids, especially lactic and acetic acids, exert a strong inhibitory effect on Gram-negative bacteria (Makras & De Vuyst, 2006). Some authors observed probiotic-mediated inhibition effect on *Escherichia coli* and *Salmonella* Enteritidis that increased proportionally to the concentration of organic acid in the medium. They also stated that low pH may not be the sole reason for the observed inhibition effects. It could however be an important condition for the passage of organic acids through the membrane to the intracellular environment, where they will accumulate and exert inhibitory activity (Fooks & Gibson, 2002). Antimicrobial compounds such as phenyllactic acid and lactic acid were effective against many Gram-negative and Gram-positive pathogenic bacteria – *Citrobacter freundii*, *Escherichia coli*, *Proteus vulgaris*, *Pseudomonas aeruginosa*, *Salmonella enterica* subsp. *enterica*, *Listeria monocytogenes*, *Staphylococcus aureus, Bacillus subtilis*, *Enterococcus faecalis* (Dal Bello *et al.*, 2007; Rodríguez *et al.*, 2012).

Because *L. plantarum* strains are effective against a variety of bacterial pathogens (including methicillin-resistant *Staphylococcus aureus* and multidrug-resistant enteroaggregative *Escherichia coli*) they can serve as alternative therapeutic agents against the corresponding infections in humans and animals (Patel *et al.*, 2013; Kumar *et al.*, 2016). For example *L. plantarum* ZDY 2013 can significantly inhibit the adhesion of enterotoxin-producing and pathogenic strains of *Bacillus cereus* on intestinal epithelial cells by inhibition, competition and displacement (Zhang *et al.*, 2016). According to another

study, *L. plantarum* ZDY 2013 pretreatment could play an important role in preventing *Helicobacter pylori* induced gastric mucosal inflammation and gastric microbiota alteration. These findings suggest that targeting gastric microbiota through oral administration of specific probiotics might be an alternative strategy to prevent *H. pylori* infection (Pan *et al.*, 2016). *L. plantarum* activity against food spoilage bacteria could be used to prolong shelf life of the food products (Amenu, 2013).

Antifungal activity of L. plantarum

According to a number of studies *L. plantarum* has inhibitory activity against many moulds and yeasts, including pathogenic and mycotoxigenic strains from the species *Aspergillus*, *Fusarium*, *Mucor*, *Candida*, etc. (Table 3). Organic acids are considered one of the main LAB compounds exerting antifungal effects (Russo *et al.*, 2016). Sangmanee & Hongpattarakere (2014) also found that the antifungal activity of *L. plantarum* K35 was pH-dependent and favourable to acidic conditions. The major antifungal substances found in that study were lactic acid, 2-butyl-4-hexyloctahydro-1H-indene, oleic acid and palmitic acid. On the other hand Niku-Paavola *et al.* (1999) observed that fungal growth was not inhibited by lactic acid and the active compounds of *L. plantarum* VTT E-78076 were benzoic acid, methylhydantoin, mevalonolactone, cyclo (glycyl-L-leucyl). The major antifungal compounds of *L. plantarum* MYS6 reported by Deepthi *et al.* (2016) were 10-octadecenoic acid, heptadecanoic acid, methyl ester, palmitic acid, stearic acid and lauric acid. The authors found that these compounds exert inhibitory effect on *Fusarium proliferatum* growth. In another study *L. plantarum* 21B showed almost 100% fungicidal activity against moulds which was due to the phenyllactic and 4-hydroxy-phenyllactic acids (Lavermicocca *et al.* 2000). There are other experiments that confirm the excellent antifungal activity of phenyllactic acid (Ström *et al.*, 2002; Dal Bello *et al.*, 2007).

According to Ryu *et al.* (2014) antifungal activity of *L. plantarum* HD1 was due to the 3-hydroxy fatty acids: 5-oxododecanoic acid, 3-hydroxy decanoic acid and 3-hydroxy-5-dodecenoic acid.

Some strains of L. *plantarum* produce cyclic dipeptides with broad spectrum of antifungal activity against moulds and yeasts, such as cyclo(Gly-Leu), cyclo (Phe-Pro), cyclo(Phe-OH-Pro), cyclo (Leu-Pro), which were considered one of the major components responsible for the antifungal activity of these strains (Niku-Paavola *et al.*, 1999; Ström *et al.*, 2002; Dal Bello *et al.*, 2007). There are some authors that found different novel peptides obtained from *L. plantarum* strains exerting antifungal activity due to damage of the cell membrane and consequent leakage of intracellular contents such as K^+ ions and ATP (Sharma & Srivastava, 2014; Muhialdin *et al.*, 2016).

In the study of wide range of potentially useful probiotic strains *L. plantarum* CECT 749 caused 99–100% aflatoxin reduction in the contaminated bread, promoted by the inhibition of the mycotoxigenic fungi. In that way the bread sample studies showed a shelf life increase of about 3–4 days (Saladino *et al.*, 2016). According to Kurhan & Çakir (2016) *L. plantarum* could safely reduce aflatoxin B_1 levels without producing any by-products. Deepthi *et al.* (2016) reported that the 61.7% reducing of fumonisin levels by *L. plantarum* MYS6 in their experiment was possibly due to binding mechanism. Some authors found that the

treatment of wheat seeds with some antimicrobial peptides produced by *L. plantarum* LR/14 prevented fungal growth even after an extended storage under laboratory conditions for around 2.5 years. All fungi examined were inhibited and spore germination was more susceptible than hyphal growth (Gupta & Srivastava, 2014).

In screening of wide range of 897 LAB isolates for antifungal activity

Table 3. Antifungal activity of *Lactobacillus plantarum* strains

Spectrum of *L. plantarum* activity	References
Moulds	
Aspergillus candidus	Coloretti *et al.*, 2007
A. carbonarius	Djossou *et al.*, 2011
A. flavus	Lavermicocca *et al.*, 2000; Yang & Chang, 2010; Ryu *et al.*, 2014; Sangmanee & Hongpattarakere, 2014; Muhialdin *et al.*, 2016; Russo *et al.*, 2016
A. fumigatus	Ström *et al.*, 2002; Sjögren *et al.*, 2003; Ryu *et al.*, 2014
A. nidulans	Ström *et al.*, 2002; Sjögren *et al.*, 2003; Ryu *et al.*, 2014
A. niger	Lavermicocca *et al.*, 2000; Dal Bello *et al.*, 2007; Gupta & Srivastava, 2014; Yasmin *et al.*, 2015; Russo *et al.*, 2016
A. ochraceus	Ryu *et al.*, 2014
A. parasiticus	Sangmanee & Hongpattarakere, 2014; Saladino *et al.*, 2016
A. petrakii	Ryu *et al.*, 2014
A. versicolor	Cheong *et al.*, 2014
Cladosporium spp.	Russo *et al.*, 2016
C. gossypiicola	Ryu *et al.*, 2014
C. herbarum	Cheong *et al.*, 2014
Endomyces fibuliger	Lavermicocca *et al.*, 2000
Eurotium repens	Lavermicocca *et al.*, 2000
E. rubrum	Lavermicocca *et al.*, 2000
Fusarium avenaceum	Niku-Paavola *et al.*, 1999
F. culmorum	Dal Bello *et al.*, 2007; Russo *et al.*, 2016
F. graminearum	Dal Bello *et al.*, 2007
F. oxysporum	Dal Bello *et al.*, 2007
F. proliferatum	Deepthi *et al.*, 2016
F. sporotrichoides	Ström *et al.*, 2002
Mucor spp.	Yasmin *et al.*, 2015
Mucor racemosus	Gupta & Srivastava, 2014
Monilia sitophila	Lavermicocca *et al.*, 2000
Penicillium spp.	Yasmin *et al.*, 2015
P. chrysogenum	Gupta & Srivastava, 2014; Russo *et al.*, 2016
P. commune	Ström *et al.*, 2002; Sjögren *et al.*, 2003; Cheong *et al.*, 2014
P. corylophilum	Lavermicocca *et al.*, 2000
P. expansum	Russo *et al.*, 2016; Saladino *et al.*, 2016
P. roqueforti	Lavermicocca *et al.*, 2000; Sjögren *et al.*, 2003; Ryu *et al.*, 2014; Muhialdin *et al.*, 2016; Russo *et al.*, 2016
P. solitum	Cheong *et al.*, 2014
Rhizopus stolonifer	Gupta & Srivastava, 2014

Table 3 (cont'd). Antifungal activity of *Lactobacillus plantarum* strains

Spectrum of *L. plantarum* activity	References
Yeasts	
Candida albicans	Ström *et al.*, 2002; Wynne *et al.*, 2004; Ryu *et al.*, 2014; Sharma & Srivastava, 2014
Debaryomyces hansenii	Ström *et al.*, 2002
Kazachstania exigua	Ryu *et al.*, 2014
Kluyveromyces marxianus	Ström *et al.*, 2002; Sjögren *et al.*, 2003
Pichia anomala	Ström *et al.*, 2002; Sjögren *et al.*, 2003
P. kudriavzevii	Ryu *et al.*, 2014
Saccharomyces bulderi	Ryu *et al.*, 2014
S. cerevisiae	Ström *et al.*, 2002; Jiang *et al.*, 2016
S. servazzii	Ryu *et al.*, 2014
Rhodotorula mucilaginosa	Ström *et al.*, 2002; Sjögren *et al.*, 2003; Inglin *et al.*, 2015; Jiang *et al.*, 2016

against cheese spoilage moulds was found that 12 isolates possessed strong antifungal activity, and all of them were identified as *L. plantarum*. Further studies indicated that all *L. plantarum* isolates prevented the visible growth of *Penicillium commune* FRR 4117 on cottage cheese by 14–25 days longer than cottage cheese without added LAB with antifungal activity (Cheong *et al.*, 2014).

L. plantarum LR/14 showed potent fungicidal activity against *Candida albicans* SC5314 by affecting cell viability, membrane permeability and biofilm formation, thereby the authors suggested this strain as a probable natural candidate therapeutic agent (Sharma & Srivastava, 2014). Some authors reported powerful inhibitory activity of tetracycline-resistant *L. plantarum* strain against *Candida albicans* that may make this probiotic useful for improved management of yeast-related conditions such as thrush and irritable bowel syndrome (Wynne *et al.*, 2004). Also, administration of *L. plantarum* is sometimes helpful for reducing the clinical symptoms and prevention of fungal infections (De Seta *et al.*, 2014).

CONCLUSIONS

Based on a wide range of investigations, *L. plantarum* should be considered an important LAB species with excellent antimicrobial activity. Because of that some *L. plantarum* strains can be used as effective biopreservatives in food industry or supporting therapeutic agents in treatment of infections caused by susceptible microorganisms. Antimicrobial compounds produced by *L. plantarum* such as bacteriocins and organic acids, could also be applied as alternatives of preservatives and therapeutics.

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