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1 **How fermentation by lactic acid bacteria can address safety issues in legumes food**
2 **products?**

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24 **Abstract**

25 Fermented Asian foods have recently gained popularity, crossing from Asian communities to
26 mainstream markets, in many western countries. However, less attention has been paid to the
27 safety of these foods. In South-East Asia fermented products are still produced following
28 traditional methods. Therefore, consumers are not confident in their microbial safety. The
29 challenges awaiting fermentation in South-East Asia are thus to improve safety and quality in
30 a sustainable system producing tasty and typical fermented products. A possible solution
31 could be the use of starter cultures able to increase the safety of food stuffs. Starters could
32 also help to standardize the production process and reduce ripening times. The current review
33 addresses the role of lactic acid bacteria on the microbiological and chemical safety of Asian
34 legume based fermented products. In particular, their role in the reduction of anti nutritional
35 compounds (e.g. phytates) and protein allergenicity is discussed. Moreover, starters can
36 inhibit the development of amino acid decarboxylating microbes preventing the accumulation
37 of biogenic amines, they can also be useful to reduce the accumulation of mycotoxins and
38 inhibit pathogens' development. Finally, their role in the degradation of pesticides is
39 analyzed.

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41 **Key words:** legumes, lactic acid bacteria, phytates, biogenic amines, mycotoxins, food safety

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50 **1. Introduction**

51 The food system is facing a crisis as consumers are confused by ambivalent information
52 arising all along the food chain. Plant products bring on the one hand vitamins and
53 micronutrients, they have a positive impact on the environment but on the other hand, they
54 might contain non-neglectable amounts of antinutritional factors (ANFs), toxic chemicals and
55 toxins. For their culture, agroindustry promotes the facilitated culture of GMO while scientific
56 studies reveal that the use of pesticide-resisting varieties results in many risks, including the
57 increase in the level of pesticide in culture, in the soil and, ultimately, in the food (Bonny
58 2016; Tsatsakis, Nawaz et al. 2017)). Some of these issues might find solutions in the future
59 by the selection of low ANF-varieties, by improving cultural techniques, decreasing the use of
60 chemicals, developing storage techniques avoiding mold contamination etc. but this will take
61 time, especially in South-East Asia where farmers are often not enough trained and have
62 economic limitations to implement the required changes in culture practices. Microorganisms
63 functionalities in fermented foods can bring several advantages to consumers (Tamang et al.,
64 2016). As an efficient, rapid and low cost solution to nutritional and food safety concerns, the
65 use of bio-remediation starters can be added to these benefits and this will be discussed in the
66 present work with a special focus on legumes.

67

68 **2. Fermented leguminous in South-East Asia**

69 Legumes such as soybeans, black beans, green beans, peanuts... are common ingredients in
70 South-East Asia for food production. They are popular for various reasons. In one hand, when
71 grown, they have the possibility to supply nitrogen to the soil through a mycorrhizal
72 association that makes this family of plant an actor of rotations in organic agriculture. On the
73 other hand, their protein content is also very high making them good nutritional candidates to
74 replace meat or milk, which production is an important source of greenhouse gas, and a big

75 consumer of plant and water resources especially in developing countries (Tubiello, 2018). In
76 particular, soybeans are most used for the production of traditional fermentation products such
77 as fermented soybean paste (*Ban Tuong*, *Cu Da Tuong* – Vn, *Nam Dan Tuong* – Vn, *Sieng* –
78 Kh), fermented soybean curd (*Chao* – Vn), *Tauxi* – *Ha Giang Dau Xi* – Vn), alkaline
79 fermentation of soybeans (natto-like) (*Thua Nao* – Th). Fermentation of these beans can have
80 an important nutrient and health impact (Cao et al. 2019; Jayachandran & Xu, 2019).
81 However, production of traditional fermentation products in South-East Asia is now managed
82 by experience, produced mainly by manual households, with rudimentary production
83 equipment, mostly fermented by endogenous microorganisms. Raw materials as well as
84 technologies have not been standardized. These products are characterized by the local
85 cultural identity. Despite their important sensorial role in Asian food, bringing for instance the
86 umami taste to the meals (Hajeb & Jinap, 2015), production management and quality
87 measurement are needed to improve quality and minimize food safety hazards. Food safety
88 issues in traditional fermented food from South-East Asia have been reviewed recently (Anal
89 et al., 2020) and soybeans, as a protein-rich matrice, are exposed to a biogenic amine risk
90 (Park et al., 2019).

91 Lactic acid bacteria (LAB) are usually not considered as the most important bacteria in
92 traditional fermentation of legumes although they have an important role and are numerous in
93 the vietnamese *tuong* and in the cambodian *sieng*.

94

95

96 **3. Antinutritional factors: can metabolic properties of LAB respond the challenges?**

97

98 Anti-nutritional factors (ANFs) are one of the main limitations for the development of
99 legume-based foods. Since the early 80's, spontaneous fermentation, generally household, has

100 been reported to degrade some leguminous ANFs such as phytates, trypsin inhibitors and
101 lectins (Chompreeda & Field, 1984a; Reddy & Pierson, 1994). Most of the analyzed
102 fermented soy derivatives contain very small amount of trypsin inhibitors and isoflavones,
103 compared to the raw soybean, but still contain phytates (Anderson & Wolf, 1995). However,
104 it was not clear if microorganisms, including lactic acid bacteria (LAB) and yeasts, played an
105 important role and even less what was their way of action. Hence, controlled
106 lactofermentations were carried out. For instance, Sindhu and Khetarpaul (2001)
107 demonstrated that LAB (*Lactobacillus casei* and *Lactobacillus plantarum*) can reduce
108 phytates, polyphenols and trypsin inhibitors in a food mixture containing green grams, with a
109 higher effect when inoculated after a first fermentation with yeasts (*Saccharomyces*
110 *boulardii*). However, LAB did not seem to have any effect on agglutinins (also called lectins)
111 (Ayyagari et al., 1989; Barkholt et al., 1998; Motarjemi & Nout, 1996). Accurate
112 characterizations of LAB activities are underway with the objective to develop appropriate
113 starters and processes, particularly for tannins and phytates removing.

114 Metabolism of tannins or other polyphenols by LAB has been characterized only in a few
115 plant fermentations including tempeh (Starzyńska-Janiszewska et al., 2014) and sorghum
116 (Svensson et al., 2010). Among LAB, *L. plantarum*, *Lactobacillus paraplantarum*,
117 *Lactobacillus pentosus* seem to be the only species capable of degrading hydrolysable tannins
118 through a tannase activity (tannin acyl hydrolase, EC 3.1.1.20) which hydrolyzes ester bounds
119 of tannic acid, thus releasing glucose and gallic acid (Osawa et al., 2000; Vaquero et al., 2004;
120 Rodriguez et al., 2009). Most of tannase producers were found in fermented vegetables but
121 also in human feces. In *L. plantarum*, tannase is very well characterized. Its activity was
122 demonstrated and characterized by Rodríguez et al. (2008) and genetic analysis showed it
123 constitutes a novel family of tannases (Iwamoto et al., 2008). LAB tannases are intracellular.
124 A *L. plantarum* strain has been reported to produce a very efficient tannase during anaerobic

125 fermentation (Aguilar-Zárate et al., 2015). Genes involved in tannins degradation are
126 regulated in a coordinated way and are inducible by tannin and other phenolic compounds
127 (Reveron et al., 2017). Characterization of fermented cassava LAB allowed identifying
128 uncommon tannase producers such as *Weissella cibaria* and *Leuconostoc mesenteroides* ssp.
129 *mesenteroides* (Kostinek et al., 2007).

130 Degradation of phytates during food process is very inconstant, depending on the process
131 (soaking, heating, milling ...) and on the plant species (Gibson et al., 2006). Soaking and
132 germination can activate plant endogenous phytases in most cereals and legumes (Holzapfel,
133 1997). The role of endogenous plant phytases during fermentation is still under debate. For
134 some authors, phytate reduction is rather the consequence of plant phytases activation during
135 fermentation than of microbial phytases (Reale et al., 2007; Shirai et al., 1994). Indeed, LAB
136 decrease and thus optimize the pH for plant phytases that are more active between pH 5 and
137 pH 4 (Gänzle et al., 2014). Moreover, production of organic acids by LAB could play a
138 synergic effect by complexing with minerals from phytates, thus making them more
139 accessible for phytases (Maenz et al., 1999). On the contrary, other authors claim that phytase
140 activity is very variable depending on the plant species, thus plant phytase activities would not
141 be sufficient in most fermentations (Cossa et al., 2000).

142 Phytases have been found in yeasts, fungi and bacteria. Generally, they are intracellular.
143 Bacterial phytases have been detected in various ubiquitous genera such as *Bacillus*,
144 *Pseudomonas*, *Klebsiella*, *Enterobacter*, *Escherichia* and in anaerobic ruminal bacteria
145 (Konietzny & Greiner, 2002). A few LAB strains have been shown to degrade, at least
146 partially, phytates. The strains belonged to *Pediococcus pentosaseus* in millet and soya
147 (Raghavendra et al., 2011), *Leuconostoc mesenteroides*, *L. plantarum*, *Lactobacillus*
148 *acidophilus* and *P. pentosaseus* in wheat (Lopez et al., 2000; Cizeikiene et al., 2015), some
149 *Lactobacillus* species in soy milk (Tang et al., 2010), *L. acidophilus*, *Lactobacillus buchneri*

150 and *L. plantarum* in lupin (Camacho et al., 1991; Fritsch et al., 2015), *Streptococcus*
151 *thermophilus* and *Bifidobacterium infantis* in co-fermentation in soymilk (Lai et al., 2013).

152 A few studies aimed to screen phytase activities among LAB strains. Anastasio et al. (2010)
153 have found 29 phytase-producers among 150 LAB, most of which isolated from wheat
154 fermentation, whereas Songré-Ouattara et al. (2008) have found 30 among 155 isolated from
155 millet fermented gruel. According to these two works, one can expect about 20% of phytases
156 producers among LAB isolated from plant fermentation, with the highest activities for some
157 *L. plantarum*, *Enterococcus faecium* and *Lactobacillus fermentum* strains. These studies
158 constitute preliminary reports that have to be strengthened. Indeed, another study has
159 highlighted the importance of the substrate used for the screening since on the 40 tested LAB
160 strains able to degrade calcium phytates, only two strains (*Pediococcus pentosaceus*) can
161 degrade sodium phytates (Raghavendra et al., 2009). In addition, Fredrikson et al. (2002)
162 warned about indirect methods to detect phytates and media composition for the screening.
163 They did not observe reliable results for LAB. It is likely that some LAB species are
164 considered as non- or low- phytase producers because the screening conditions do not permit
165 phytase production in bacteria (Konietzny & Greiner, 2002).

166 Some studies have been carried out with tighter methods. Sreeramulu et al. (1996) have
167 reported that *Lactobacillus amylovorus* was a good producer of extracellular phytases and that
168 extracellular activity was also detected for *L. acidophilus*, *L. plantarum*, *Lactobacillus*
169 *delbrueckii* and *L. casei*. They did not detect any production with *Lactococcus lactis* or
170 *Lactobacillus helveticus*. Moreover, Zamudio et al. (2001) have reported the ability of six
171 strains of LAB (*P. pentosaceus*, *Leuconostoc mesenteroides*, *L. casei*, *L. fermentum*, *L.*
172 *delbrueckii* and *L. plantarum*) to partially degrade phytate (from 6 to 11%). Whereas no
173 intracellular and low extracellular phytase activities were measured, they proved that phytate
174 degradation was due to a non-specific acid phosphatase. Palacios et al. (2005) have come to

175 the same conclusion by characterizing a *L. pentosus* non-specific acid phosphatase (EC
176 3.1.3.2) which was able to hydrolyze phytates. De Angelis et al. (2003) have gone further by
177 characterizing an intracellular phytase of *L. sanfranciscensis* at the protein level. They did not
178 identify the corresponding gene. This strain decreased phytate content of almost 75% in
179 sourdough after an 8 h-incubation.

180 Several groups have identified and characterized efficient phytases in the *Bifidobacterium*
181 genera (Haros et al., 2007; Tamayo-Ramos et al., 2012; García-Mantrana et al., 2015) but this
182 genus does not fit with legumes fermentation mainly because it is strict anaerobic and
183 fastidious. To overcome this limitation, García-Mantrana et al. (2016) succeeded in
184 expressing active bifidobacterial phytases in *L. casei*. Nevertheless, in sourdough, the
185 bacterial activity was low, compared to the activated plant phytases.

186 Actually, identifying new LAB phytase activities based on phenotypical screening seems
187 hazardous. Otherwise, *in silico* analysis of LAB genomes based on known bacterial phytases
188 (*Bacillus*, *Escherichia* spp) does not predict any phytase (personal data). Even bifidobacterial
189 phytases found by García-Mantrana et al. (2015) are very specific. Thus, molecular screening
190 is not feasible for LAB. However, characterizing enzymatic activities and identifying the
191 corresponding genes in LAB strains already highlighted would be very informative to know if
192 specific or non-specific phytases exist in some LAB strains and if these phytases would be
193 efficient in reducing the phytate content in fermented legumes.

194

195 **4. Decrease of protein allergenicity through LAB-mediated hydrolysis**

196 The main legume allergens are the proteins. These complex structures are difficult to degrade.
197 The selection of legumes natural variants or the use of specific biotechnological processes can
198 eliminate these particular proteins. However, they might also induce some side effects such as
199 an increase in the protein synthesis pathways of the seed and the synthesis of other proteins

200 that might be allergenic as well (Nowak-Wegrzyn & Fiocchi, 2009 ; Mils et al., 2009 ;
201 Kroghsbo et al., 2014; Rahaman et al., 2016).

202 Plant proteins exhibits low digestibility compared to animal proteins. Poor protein
203 digestibility can cause gastrointestinal disorders that may result in fecal excretion of proteins.
204 Therefore, increasing protein digestibility could reduce the levels of undigested proteins
205 which can potentially cause food allergies due to poor absorption in the gut (Untersmayr &
206 Jensen-Jarolim, 2008). Several studies have showed that LAB fermentation increases the
207 digestibility of plant proteins (El-Haget al., 2002; Pranoto et al., 2013).

208 For example, during fermentation of lupin and soybean, protein digestibility is improved by
209 using LAB cultures such as *Lactobacillus sakei* KTU05-6, *Pediococcus acidilactici* KTU05-
210 07 and *P. pentosaceus* KTU05-8. This improvement is due to the role of microbial proteolytic
211 enzymes. These enzymes partially hydrolyze these proteins into peptides and free amino
212 acids. These simple and soluble products are easier to digest than the whole protein (Bartkiene
213 et al., 2013a; Bartkiene et al., 2013b; Aguirre et al., 2014). Fermentation of soybean meal
214 with *L. plantarum* or *Bifidobacterium lactis* showed a significant increase in the total amino
215 acids and a low immunoreactivity. Thus, the use of fermentation to reduce or eliminate
216 allergenicity of soy products represents an interesting opportunity to produce hypoallergenic
217 food products from legumes (Song et al., 2008a; Song et al., 2008b).

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219

220 **5. Lactic acid bacteria as biopreservation agent against pathogenic bacteria**

221 Besides decreasing antinutritional factors (ANFs) and allergy, lactic acid bacteria can fulfill a
222 task of biopreservation. This word can be defined as the extension of shelf-life and food
223 safety by the use of natural or controlled microbiota and/or their antimicrobial compounds
224 (Ananou, Maqueda et al. 2007).

225 Fermentation by lactic acid bacteria (LAB) is one of the most common methods of food
226 biopreservation. In this process, organoleptic properties (unique flavor, aroma compounds) of
227 products are also developed and improved. This is an important advantage of fermentation
228 compared to non-fermented products that have to be biopreserved without any organoleptic
229 impact.

230 In South-East Asia, biopreservation strategies have been designed to avoid pathogens
231 contamination in various products, although fermented meat as well as vegetables other than
232 legumes, two classes being often considered as the riskiest products. For instance, (Phan,
233 Tang et al. 2017) determined the diversity of LAB in 25 samples of meat and vegetable
234 fermented products in Vietnam including *dua gia* (bean sprouts), *dua cai* (cabbage), *mang*
235 *chua* (bamboo shoots), *nem chua* (uncooked pork) and *tre* (cooked pork). The results showed
236 that the major species found in vegetable-based products (*L. plantarum*, *L. fermentum*, and *L.*
237 *helveticus*) were different from those identified in meat-based products (*P. pentosaceus*,
238 *Weissella cibaria*, and *Lactococcus lactis*) (Phan, Tang et al. 2017). The LAB ranged
239 approximately from 10^6 to 10^9 CFU/g, depending on the food items (Phan, Tang et al. 2017).

240 In the case of legumes, it is important to use bacteria that can develop easily on these plant
241 matrices rich in proteins but also to take into account the specificities of contaminations. From
242 the field, legumes are likely to bring with them sporulating bacteria. Later, fungi can develop
243 and produce mycotoxins. Finally, depending on the handling of the products, pathogens can
244 occur through cross-contamination from meat or vegetables. The range of possible
245 contaminants is thus rather wide. The inhibitory mechanisms of biopreservation by LAB
246 against spoilage organisms are destabilization of cell membrane and subsequent interference
247 with the proton gradient, inhibition enzyme activity and creation of reactive oxygen species.
248 LAB strains are able to produce various antimicrobial substances such as low-molecular
249 weight metabolites (reuterin, reutericyclin, diacetyl, fatty acids), hydrogen peroxide,

250 antifungal compounds (propionate, phenyl-lactate, hydroxyphenyl-lactate and 3-hydroxy fatty
251 acids), and bacteriocins that may be exploited in the biopreservation of foods (Siedler, Balti et
252 al. 2019).

253 There is a wide number of bacteriocins produced by LAB and they can be classified into three
254 classes. Class I (Lantibiotics), class II (Non-Lantibiotics) and class III (Big peptides)
255 depending on their chemical and genetic characteristics. The antibacterial activity of nisin, the
256 most studied lantibiotics, has been demonstrated against *Listeria* sp., *Micrococcus* sp. and
257 sporulating bacteria such as *Bacillus* sp. and *Clostridium* sp. (Parada, Caron et al. 2007).

258 Nguyen et al. (Nguyen, Elegado et al. 2009) isolated the LAB from nem chua and determined
259 their antimicrobial activity against pathogenic and sporulating strains such as *Bacillus cereus*,
260 *L. plantarum* JCM 1149, *Listeria monocytogenes*, *E. coli*, and *Salmonella* Typhimurium. Five
261 strains NH3.6, NT1.3, NT1.6, NT2.9, and NT3.20 showed a broaden antimicrobial activity
262 against both pathogenic Gram-positive *B. cereus* and *L. monocytogenes*, and gram-negative *E.*
263 *coli* with the zone of inhibition ranging from 1,5-6 mm (D-d), however no inhibitory effect
264 against *S. Typhimurium* was detected (Nguyen, Elegado et al. 2009). *L. plantarum* HA2,
265 HA3, HA5, HA8 and HA9 and *L. fermentum* HA6, HA7 and HA10 isolated from Vietnamese
266 fermented vegetables showed a strong and broad antifungal activity against 7 out of 11
267 indicator mold and yeast strains (*Aspergillus terreus*, *A. fumigatus*, *A. niger*, *Absidia*
268 *corymbifera*, *Paecilomyces lilacinus*, *Geotrichum candidum*, *Fusarium* sp., *Scopulariopsis*
269 *brevicaulis*, *Curvularia lunata*, *Penicillium* sp., and *Candida albicans*) (Ho, Luo et al. 2009).
270 From these two collections, biopreservatives LAB could be investigated for the specific
271 problems of legume fermented products.

272 **6. Biogenic amines, fermentation may be the risk, but also the solution**

273 Microbial fermentation has been employed for millennia by mankind to prolong shelf life and
274 improve texture and flavour of food stuffs. However, protein-rich raw materials can be a

275 source of aminoacids which can be converted into biogenic amines (BAs) by microorganisms.
276 Biogenic amines are nitrogenous compounds of low molecular weight occurring in several
277 fermented foods. The main BAs present in foods are histamine, tyramine, tryptamine,
278 putrescine, cadaverine, and phenylethylamine (Gardini et al., 2016). Their accumulation is
279 mainly due to microbial decarboxylation of aminoacids through the action of decarboxylases
280 which remove the carboxyl group with the formation of the corresponding amine and CO₂, or
281 through the amination and transamination of aldehydes and ketones (Alvarez et al., 2014).
282 These compounds can cause toxic effects in consumers with several symptoms such as
283 nausea, flushes, heart palpitation, headache, red rash, oral burning, and hypo- or hypertension
284 which are more severe in consumers with an inefficient detoxification system and depend on
285 the amount and type of BA ingested (Ladero et al., 2010).

286 Biogenic amines are produced not only by Gram-positive and Gram-negative bacteria, but
287 also by yeasts and molds (Gardini et al., 2016). However, lactic acid bacteria (LAB) are
288 considered as the main BA producers in fermented foods and *Enterococcus*, *Lactobacillus*,
289 *Streptococcus*, *Lactococcus*, *Oenococcus*, *Pediococcus*, *Weissella*, *Carnobacterium*,
290 *Tetragenococcus*, *Leuconostoc*, *Sporolactobacillus* are the main genera showing this trait
291 (Barbieri et al., 2019). BAs production is a strain specific feature and some studies revealed
292 that the involved enzyme is encoded by unstable plasmids (Lucas et al., 2005; Satomi et al.,
293 2008). Therefore, horizontal gene transfer is essential to disseminate this ability in LAB
294 (Lucas et al., 2005; Satomi et al., 2008).

295 Although the factors influencing BAs production (e.g. temperature, salt concentration, and
296 pH) are well known, it is difficult to prevent their accumulation in fermented foods, since the
297 fermentation conditions cannot be easily modified and the aminobiogenic ability is strain-
298 dependent. Several strategies have been proposed to prevent BAs accumulation in foods;
299 however, they can decrease the nutritional value and the organoleptic features of foods (for a

300 review see Naila et al., 2010). In the case of legumes, the boiling allows the elimination of
301 BAs, unfortunately, for sprouted legumes, this approach permits only a reduction of their
302 content (Shalaby, 2000). One of the most promising strategies is the use of amine oxidizing
303 starter cultures. Three different classes of oxidases have been described: flavin-containing
304 monoamine oxidases (FlavAO), copper containing amine oxidases (CuAO), and multi-copper
305 oxidases (MCO). They catalyze the oxidative deamination of BAs forming the corresponding
306 aldehydes, hydrogen peroxide and ammonia (Guarcello et al., 2016). Kim et al. (2012)
307 isolated strains of *Bacillus subtilis* and *Bacillus amyloliquefaciens* from fermented soybean
308 foods. They observed the ability of *B. subtilis* to degrade putrescine and cadaverine and of *B.*
309 *amyloliquefaciens* to oxidize histamine and tyramine. Similarly, Kang et al. (2017) showed
310 the ability of *B. subtilis* and *B. amyloliquefaciens* strains to reduce tyramine in
311 Cheonggukjang. Eom et al. (2015) isolated from buckwheat sokseongjang, a Korean
312 traditional fermented soybean food, 3 strains (*B. subtilis* HJ0-6, *B. subtilis* D'J53-4, and *B.*
313 *idriensis* RD13-10) which were not only able to degrade histamine and tyramine but also
314 unable to produce them. Finally, Lee et al. (2016) proposed the use of *L. plantarum* strains to
315 reduce BAs content during Miso fermentation.

316 The possibility to select new amine oxidizing starter cultures could represent a promising
317 strategy to reduce BAs content in legumes based fermented foods where traditional methods
318 are inadequate or it is necessary to eliminate BAs already formed during the fermentation
319 process.

320

321 **7. Mycotoxins in leguminous: can fermentation degrade what fungi have made?**

322 Fermentation is the chemical process which converts substrates into product(s) by using
323 microorganisms for example fungi, yeast and bacteria. There are many undesirable substances
324 contaminating foods and feeds that are harmful to human and animal health. These include

325 mycotoxins, which are widely present in food and feeds commodities. Microorganisms
326 including fungi, yeast, and bacteria are able to eliminate mycotoxins. Additionally, various
327 studies have been extensively reporting about their mycotoxin degradation mechanisms such
328 as cell wall-binding, enzyme degrading or structure modification. However, these
329 mechanisms of actions depend on strains of microorganisms. (El-Sharkawy & Abul-Hajj,
330 1988; Kakeya et al., 2002; Takahashi-Ando et al., 2002; Vekiru et al., 2010; El-Nezami et al.,
331 2002; Zhao et al., 2015). Lactic acid bacteria (LAB) can be extensively found in various
332 fermented foods (meat, vegetable, and milk). They are widely used to ferment and preserve
333 foods and feeds in place of chemical preservatives due to their lower cost and better safety.
334 They can produce antimicrobial and antagonistic compounds for the control of pathogenic
335 bacteria/fungi and spoilage microflora. Additionally, the LAB are widely applied to reduce
336 mycotoxins. The capability of LAB to remove mycotoxin has been reported more than two
337 decades ago for several toxins such as aflatoxin B₁ (Haskard et al., 2000; El-Nezami et al.,
338 2002; Lahtinen et al., 2004; Taheur et al., 2017), zearalenone (El-Nezami et al., 2004;
339 Adunphatcharaphon et al., 2013; Long et al., 2012), ochratoxin A (Fuchs et al., 2008),
340 fumonisins (Niderkorn et al., 2009), and patulin (Fuchs et al., 2008; Wang et al., 2015).
341 Numerous LAB (*Lactobacillus rhamnosus*, *L. plantarum*, *L. casei*, *L. curvatus*, *L.*
342 *coryniformis*, *L. brevis*, *L. mucosae*, and *L. pentosus*) exhibit mycotoxin reduction ability in
343 which binding is their main mechanism. (El-Nezami et al., 2002; El-Nezami et al., 2004;
344 Long et al., 2012). The cell wall of LAB has the typical Gram-positive structure made of a
345 complex assemblage of glycopolymers and proteins. It consists in a thick peptidoglycan that
346 surrounds the cytoplasmic membrane and is decorated with proteins, polysaccharides, and
347 teichoic acids (Chapot-Chartier et al., 2014; Delcour et al., 1999). The sugars and amino acids
348 in glycopolymer or protein structures onto bacterial cell wall is different in each species of
349 bacterial cell (Chapot-Chartier et al., 2014). Moreover, polysaccharides have been suggested

350 to be the important elements responsible for the binding of aflatoxin B₁ (Haskard et al., 2000)
351 and fumonisins (Niderkorn et al., 2009) by LAB. Polysaccharides in Gram-positive bacteria
352 can be found in 3 parts: peptidoglycan, teichoic acids, and natural polysaccharides which
353 include exopolysaccharides, capsular polysaccharides, and cell wall polysaccharides.
354 Bacterial polysaccharides exhibit great diversity, not only in sugar composition but also in
355 linkage, branching, and substitution (Chapot-Chartier et al., 2014). This means that
356 peptidoglycan and teichoic acids are also related to mycotoxin reduction and the difference in
357 mycotoxin removal capacity in each bacterial strain arises from the diversity of
358 polysaccharides. Hernandez-Mendoza et al. (2009) exhibited that the protoplast of
359 *Lactobacillus reuteri* and *L. casei* Shirota also showed the capacity to reduce aflatoxin B₁ *in*
360 *vitro*. Both data implied that lipids were one of the components which were able to attach to
361 the mycotoxin. All of these studies supported that the mycotoxin removal by bacterial cell
362 was strain specific because of the diversity of each element structures onto bacterial cell wall,
363 which includes proteins, polysaccharides, and lipids. Therefore, this class of microorganism
364 has demonstrated great potential in fungal inhibition and mycotoxin removal in fermented
365 legumes food products.

366

367 **8. Fermentation against chemicals from agriculture**

368 The presence of chemicals and pesticides in plant products is a growing societal concern.
369 Some studies point out that following recommendation to increase the dietary uptake of fruit
370 and vegetables means often increasing the uptake of chemicals. For instance in Brasil, the
371 cumulative intake of organophosphorus and carbamate pesticides by high consumers of fruits
372 and vegetables has been evaluated to represent up to 169% of the Acute reference dose
373 (ARfD) (Caldas and Jardim 2011). This type of data gives rise to a debate whether benefits of
374 eating vegetarian products are higher than risks (Richter ED and N. 2002). In any case, there

375 is a consensus that the level of contamination by pesticide has to be significantly decreased.
376 However, despite several Integrated Pest Management (IPM) programs, decreasing the use of
377 pesticides in agriculture and therefore in food products is difficult. One transient possibility
378 (before an agricultural control of persistent organic pollutants) is to degrade pesticides or
379 chemical degradation products through fermentation.

380 Considering the diversity of the earth microbiome, many chemicals can be transformed.
381 However, when limiting the diversity to the safe bacteria that can be encountered in fermented
382 products, the choice of biocatalytic activities is narrowed. Degradation of pesticides during
383 fermentation has already been analyzed in several studies showing a good potential of
384 degradation of organophosphorus insecticides like chlorpyrifos during the fermentation of
385 Kimchi by strains belonging to *L. mesenteroides*, *L. brevis*, *L. plantarum*, and *L. sakei* (Cho et
386 al., 2009). *Lactobacillus brevis* was also seen as an active catalyst against the same family of
387 products during the fermentation of milk products (Zhang et al., 2014). The degradation of
388 organochlorine pesticides has also been investigated in milk during yogurt and cheese
389 production showing the effect of starters (Duan et al., 2018). Other examples show the
390 capability of *Micrococcus varians* to degrade DDT to DDD and lindane to 2,4-, 2,5-, 2,6- and
391 3,4-dichlorophenol; 2,3,4- and 2,3,5-trichlorophenol; hexachlorobenzene; and
392 pentachlorophenol. However in sausage, the degradation was only of 10 to 18% during the 72
393 h of sausage fermentation (Abou-Arab, 2002).

394 With the use of soy from the world market (mainly glyphosate resistant genetically-modified
395 soy) to manufacture fermented soy in South-East Asia, it is likely that glyphosate is a main
396 herbicide that has to be degraded although it can be combined with several other chemicals.
397 The screening of strains able to degrade pesticides from fermented food is thus a potential
398 way to decrease the contamination of foods by chemicals. Up to now, this subject of
399 bioremediation of pesticides has been more focused on environmental microbiomes (Zhan et

400 al., 2018) and the screening can also be extended to environmental lactic acid bacteria strains
401 as in the following example for which *Lactococcus lactis* subsp. *lactis* able to degrade
402 dinitrotoluene isomers has been isolated from earthworm intestine (Shin et al., 2005).

403 **9. Conclusion**

404 Lactic acid bacteria are more and more used as a biopreservation agent against the
405 development of pathogens and spoilage microorganisms in food products. They have also a
406 potential to metabolize many compounds that are present in legumes and should be avoided in
407 food products (Figure 1). They can thus decrease antinutritional factors and allergens as well
408 as chemicals and pesticides used for culture. They can eventually remediate the presence of
409 toxins from other microorganisms like mycotoxins and can oxidize biogenic amines.
410 Although they already fulfill these roles in many fermented products, their role for
411 bioremediation is still underutilized due to a lack of knowledge about precise genes and
412 mechanisms involved. The screening of LAB functions helping to decrease the concentration
413 of all these potentially toxic molecules is thus of great potential to improve food safety of
414 products, not only fermented. Some questions remain, as for instance how to orient
415 metabolism towards the targeted compounds? Can we find, in LAB diversity, strains able to
416 degrade all types of compounds? Is the metabolization of toxic compounds sufficient to
417 decrease significantly the risk?

418 Although decreasing contamination is the first food safety strategy, lactic acid bacteria show a
419 great potential through bioremediation functionalities that can help to decrease consumers'
420 exposition to many toxic compounds. Some strains have already been identified in fermented
421 foods but the development of starters with these functionalities has still to be developed.

422

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429

430 **References**Abou-Arab, A. A. K. (2002). Degradation of organochlorine pesticides by meat
431 starter in liquid media and fermented sausage. *Food and Chemical Toxicology*, 40, 33-41.

432

433 Adunphatcharaphon, S., Petchkongkaew, A. & Visessanguan, W. (2013). *In Vitro* Screening
434 of Potential Plant-Derived Lactic Acid Bacteria for Zearalenone Removal. TSB 2013
435 Programme & Book of Abstracts the 25th Annual Meeting of The Thai Society for
436 Biotechnology and International Conference: Agro-Industrial Biotechnology for Global
437 Sustainable Prosperity. October, 16th-19th, 2013. The Emerald Hotel, Bangkok, Thailand, P-
438 08-017.

439

440 Aguilar-Zárate, P., Cruz, M. A., Montañez, J., Rodríguez-Herrera, R., Wong-Paz, J. E.,
441 Belmares, R. E., & Aguilar, C. N. (2015). Gallic acid production under anaerobic submerged
442 fermentation by two bacilli strains. *Microbial Cell Factories*, 14, 209.

443

444 Aguirre, L., Hebert, E. M., Garro M. S., & de Giori, G. S. (2014). Proteolytic activity of
445 *Lactobacillus* strains on soybean proteins. *Food Science and Technology*, 59, 780-785.

446

447 Alvarez, M. A., & Moreno-Arribas, M. V. (2014). The problem of biogenic amines in
448 fermented foods and the use of potential biogenic amine-degrading microorganisms as a
449 solution. *Trends in Food Science & Technology*, 39, 146–155.

450

451 Anal, A.K., Perpetuini G., Petchkongkaew A., Tan R., Avallon S., Tofalo R., Nguyen H.V.,
452 Chu-Ky S., Ho P.H., Phan T.T., Waché Y. (2020). Food safety risks in traditional fermented
453 food from South-East Asia. *Food Control*, 106922.

454

455 Ananou, S., Maqueda, M., Martínez-Bueno, M., Gálvez, A., & Valdivia, E. (2007).
456 Bactericidal synergism through enterocin AS-48 and chemical preservatives against
457 *Staphylococcus aureus*. *Letters in Applied Microbiology*, 45, 19-23.

458

459 Anastasio, M., Pepe, O., Cirillo, T., Palomba, S., Blaiotta, G., & Villani, F. (2010). Selection
460 and use of phytate-degrading LAB to improve cereal-based products by mineral solubilization
461 during dough fermentation. *Journal of Food Science*, 75, M28-35.

462

463 Anderson, R. L., & Wolf, W. J. (1995). Compositional changes in trypsin inhibitors, phytic
464 acid, saponins and isoflavones related to soybean processing. *The Journal of Nutrition*, 125,
465 S581.

466

467 Ayyagari, R., Rao, B. N., & Roy, D. N. (1989). Lectins, trypsin inhibitors, BOAA and tannins
468 in legumes and cereals and the effects of processing. *Food Chemistry*, 34, 229-238.

469

470 Bakkali, F., Averbeck, S., Averbeck, D., & Idaomar, M. (2008). Biological effects of essential
471 oils-a review. *Food and Chemical Toxicology*, 46, 446-475.

472

473 Barkholt, V., Jergensen, P. B., Sørensen, D., Bahrenscheer, J., Haikara, A., Lemola, E., &
474 Frøkiær, H. (1998). Protein modification by fermentation: effect of fermentation on the
475 potential allergenicity of pea. *Allergy*, 53, 106-108.

476

477 Bartkiene, E., Juodeikiene, G., Vidmantiene, D., Zdunczyk, Z., Zdunczyk, P., Juskiewicz, J.,
478 Cizeikiene, D., & Matusevicius, P. (2013a). Influence of diets to Wistar rats supplemented
479 withsoya, flaxseed and lupine roducts treated by lactofermentation to improve their gut health.
480 *International Journal of Food Sciences and Nutrition*, 64,730-739.

481

482 Bartkiene, E., Schleining, G., Rekstyt, T., Krungleviciut, V., Juodeikiene, G., Vaiciulyte-
483 Funk, L., & Maknickiene, Z. (2013b). Influence of the addition of lupin sourdough with
484 different lactobacilli on dough properties and bread quality. *International Journal of Food*
485 *Science and Technology*, 48, 2613-2620.

486

487 Bonny, S. (2016). Genetically Modified Herbicide-Tolerant Crops, Weeds, and Herbicides:
488 Overview and Impact. *Environmental Management*, 57, 31-48.

489

490 Caldas, E. D., & Jardim, A. N. O. (2011). "Exposure to toxic chemicals in the diet: Is the
491 Brazilian population at risk?" *Journal of Exposure Science and Environmental Epidemiology*,
492 22 1.

493

494 Camacho, L., Sierra, C., Marcus, D., Guzman, E., Campos, R., Von Bäer, D., & Trugo, L.
495 (1991). Nutritional quality of lupine (*Lupinus albus* cv. *Multolupa*) as affected by lactic acid
496 fermentation. *International Journal of Food Microbiology*, 14, 277-286.

497

498 Cao, Z.H., Green-Johnson J.M., Buckley N.D., Lin Q.Y. (2019). Bioactivity of soy-based
499 fermented foods: A review. *Biotechnology Advances*, 37, 223-238.

500

501 Chapot-Chartier, M. P., & Kulakauskas, S. (2014). Cell wall structure and function in lactic
502 acid bacteria. *Microbial Cell Factories*. Proceedings of the 11st Symposium on Lactic Acid
503 Bacteria. Egmond aan Zee, The Netherlands. August 31-September 4, 13, S9.
504

505 Chien, H. L., Huang, H. Y., & Chou, C. C. (2006). Transformation of isoflavone
506 phytoestrogens during the fermentation of soymilk with lactic acid bacteria and
507 bifidobacteria. *Food Microbiology*, 23, 772-778.
508

509 Cho, K. M., Math, R. K., Islam, S. M., Lim, W. J., Hong, S. Y., Kim, J. M., Yun, M. G., Cho,
510 J. J., & Yun, H. D. (2009). "Biodegradation of Chlorpyrifos by Lactic Acid Bacteria during
511 Kimchi Fermentation." *Journal of Agricultural and Food Chemistry*, 57, 1882-1889.
512

513 Chompreeda, P. T., & Fields, M. L. (1984). Effects of heat and natural fermentation on amino
514 acids, flatus producing compounds, lipid oxidation and trypsin inhibitor in blends of soybean
515 and cornmeal. *Journal of Food Science*, 49, 563-565.
516

517 Cizeikiene, D., Juodeikiene, G., Bartkiene, E., Damasius, J., & Paskevicius, A. (2015).
518 Phytase activity of lactic acid bacteria and their impact on the solubility of minerals from
519 wholemeal wheat bread. *International Journal of Food Sciences and Nutrition*, 66, 736-742.
520

521 Cossa, J., Oloffs, K., Kluge, H., Drauschke, W., & Jeroch, H. (2000). Variabilities of total and
522 phytate phosphorus contents as well as phytase activity in wheat. *Journal of Agriculture in the*
523 *Tropics and Subtropics*, 101, 119-126.
524

525 De Angelis, M., Gallo, G., Corbo, M. R., McSweeney, P. L., Faccia, M., Giovine, M., &
526 Gobbetti, M. (2003). Phytase activity in sourdough lactic acid bacteria: purification and
527 characterization of a phytase from *Lactobacillus sanfranciscensis* CB1. *International Journal*
528 *of Food Microbiology*, 87, 259-270.

529

530 Delcour, J., Ferain, T., Deghorain, M., Palumbo, E., & Hols, P. (1999). The biosynthesis and
531 functionality of the cell-wall of lactic acid bacteria. *Antonie van Leeuwenhoek*, 76, 159–184.

532

533 Duan, J., Cheng, Z., Bi, J., & Xu, Y. (2018). Residue behavior of organochlorine pesticides
534 during the production process of yogurt and cheese. *Food Chemistry*, 245 119-124.

535

536 El-Hag, M. E., El-Tinay, A. H., & Yousif, N. E. (2002). Effect of fermentation and dehulling
537 on starch, total polyphenols, phytic acid content and in vitro protein digestibility of pearl
538 millet. *Food Chemistry*, 77,193–196.

539

540 El-Nezami, H., Polychronaki, N., Lee, Y. K., Haskard, C., Juvonen, R., Salminen, S., &
541 Mykkänen, H. (2004). Chemical moieties and interactions involved in the binding of
542 zearalenone to the surface of *Lactobacillus rhamnosus* strains GG. *Journal of Agricultural*
543 *and Food Chemistry*, 52, 4577-4581.

544

545 El-Nezami, H., Polychronaki, N., Salminen, S., & Mykkänen, H. (2002). Binding Rather
546 Than Metabolism May Explain the interaction of Two Food-Grade *Lactobacillus* Strains with
547 Zearalenone and Its Derivative α -Zearalenol. *Applied and Environmental Microbiology*, 68,
548 3545-3549.

549

550 El-Sharkawy, S. H., & Abul-hajj, Y. J. (1988). Microbial transformation of zearalenone:
551 Reduction, hydroxylation, and methylation products. *The Journal of Organic Chemistry*, 53,
552 515–519.

553

554 Eom, J. S., Seo, B. Y., & Choi, H. S. (2015). Biogenic amine degradation by *Bacillus* species
555 isolated from traditional fermented soybean food and detection of decarboxylase-related
556 genes. *Journal of Microbiology and Biotechnology*, 25, 1519–1527.

557

558 Fernandes, J. C., Eaton, P., Gomes, A. M., Pintado, M. E., & Xavier Malcata, F. (2009).
559 Study of the antibacterial effects of chitosans on *Bacillus cereus* (and its spores) by atomic
560 force microscopy imaging and nanoindentation. *Ultramicroscopy*, 109, 854-860.

561

562 Fredrikson, M., Andlid, T., Haikara, A., & Sandberg, A. S. (2002). Phytate degradation by
563 micro-organisms in synthetic media and pea flour. *Journal of Applied Microbiology*, 93, 197-
564 204.

565

566 Fritsch, C., Vogel, R. F., & Toelstede, S. (2015). Fermentation performance of lactic acid
567 bacteria in different lupin substrates—influence and degradation ability of antinutritives and
568 secondary plant metabolites. *Journal of Applied Microbiology*, 119, 1075-1088.

569

570 Fuchs, S., Sontag, G., Stidl, R., Ehrlich, V., Kundi, M., & Knasmuller, S. (2008).
571 Detoxification of patulin and ochratoxin A, two abundant mycotoxins, by lactic acid bacteria.
572 *Food and Chemical Toxicology*, 46, 1398–1407.

573

574 Gänzle, M. G. (2014). Enzymatic and bacterial conversions during sourdough fermentation.
575 *Food Microbiology*, 37, 2-10.
576

577 García-Mantrana, I., Monedero, V., & Haros, M. (2015). Myo-inositol hexakisphosphate
578 degradation by *Bifidobacterium pseudocatenulatum* ATCC 27919 improves mineral
579 availability of high fibre rye-wheat sour bread. *Food Chemistry*, 178, 267-275.
580

581 García-Mantrana, I., Yebra, M. J., Haros, M., & Monedero, V. (2016). Expression of
582 bifidobacterial phytases in *Lactobacillus casei* and their application in a food model of whole-
583 grain sourdough bread. *International Journal of Food Microbiology*, 216, 18-24.
584

585 Gardini, F., Zogul, Y., Suzzi, G., Tabanelli, G., & Zogul, F. (2016). Technological factors
586 affecting biogenic amine content in foods: a review. *Frontiers in Microbiology*, 7, 1218.

587 Gibson, R. S., Perlas, L., & Hotz, C. (2006). Improving the bioavailability of nutrients in
588 plant foods at the household level. *Proceedings of the Nutrition Society*, 65, 160-168.
589

590 Guarcello, R., De Angelis, M., Settanni, L., Formiglio, S., Gaglio, R., Minervini, F.,
591 Moschetti, G., & Gobbetti, M. (2016). Selection of amine-oxidizing dairy lactic acid bacteria
592 and identification of the enzyme and gene involved in the decrease of biogenic amines.
593 *Applied and Environmental Microbiology*, 82, 6870–6880.
594

595 Hajeb, P., Jinap, S. (2015). Umami taste components and their sources in Asian foods.
596 *Critical Reviews in Food Science and Nutrition*, 55, 778-791.
597

598 Haros, M., Bielecka, M., Honke, J., & Sanz, Y. (2007). Myo-inositol hexakisphosphate
599 degradation by *Bifidobacterium infantis* ATCC 15697. *International Journal of Food*
600 *Microbiology*, 117, 76-84.

601

602 Haskard, C., Binnion, C., & Ahokas, J. (2000). Factors affecting the sequestration of aflatoxin
603 by *Lactobacillus rhamnosus* strain GG. *Chemico-Biological Interactions*, 128, 39–49.

604

605 Hassan, O., & Chang, T. (2017). Chitosan for eco-friendly control of plant disease. *Asian*
606 *Journal of Plant Pathology*, 11, 53-70.

607

608 Hernandez-Mendoza, A., Guzman-de-Pena, D., & Garcia, H.S. (2009). Key role of teichoic
609 acids on aflatoxin B1 binding by probiotic bacteria. *Journal of Applied Microbiology*, 107,
610 395-403.

611

612 Ho, P.-H., Luo, J., & Adams, M. (2009). Lactobacilli and dairy propionibacterium with
613 potential as biopreservatives against food fungi and yeast contamination. *Applied*
614 *Biochemistry Microbiology*, 45, 414-418.

615

616 Holzappel, W. (1997). Use of starter cultures in fermentation on a household scale. *Food*
617 *Control*, 8, 241-258.

618

619 Inouye, S., Watanabe, M., Nishiyama, Y., Takeo, K., Akao, M., & Yamaguchi, H. (1998).
620 Antisporulating and respiration-inhibitory effects of essential oils on filamentous fungi.
621 *Mycoses*, 41, 403-410.

622

623 Iwamoto, K., Tsuruta, H., Nishitani, Y., & Osawa, R. (2008). Identification and cloning of a
624 gene encoding tannase (tannin acylhydrolase) from *Lactobacillus plantarum* ATCC 14917 T.
625 *Systematic and Applied Microbiology*, 31, 269-277.

626

627 Jayachandran M., Xu B. (2019). An insight into the health benefits of fermented soy products.
628 *Food Chemistry*, 271, 362-371.

629

630 Jiménez, N., Curiel, J. A., Reverón, I., de las Rivas, B., & Muñoz, R. (2013). Uncovering the
631 *Lactobacillus plantarum* WCFS1 gallate decarboxylase involved in tannin degradation.
632 *Applied and Environmental Microbiology*, 79, 4253-4263.

633

634 Kakeya, H., Takahashi-ando, N., Kimura, M., Onese, R., I. Yamaguchi, I., & Osada, H.
635 (2002). Biotransformation of the mycotoxin, zearalenone, to a non-estrogenic compound by a
636 fungal strain of *Clonostachys* sp. *Bioscience Biotechnology and Biochemistry*, 66, 2723-2726.

637

638 Kang, H. R., Lee, Y. L., & Hwang, H. J. (2017). Potential for application as a starter culture
639 of tyramine-reducing strain. *Journal of the Korean Society of Food Science and Nutrition*, 46,
640 1561–1567.

641

642 Kim, Y. S., Cho, S. H., Jeong, D. Y., & Uhm, T. B. (2012). Isolation of biogenic amines-
643 degrading strains of *Bacillus subtilis* and *Bacillus amyloliquefaciens* from traditionally
644 fermented soybean products. *Korean Journal of Microbiology*, 48, 220–224.

645

646 Konietzny, U., & Greiner, R. (2002). Molecular and catalytic properties of phytate-degrading
647 enzymes (phytases). *International Journal of Food Science & Technology*, 37, 791-812.

648

649 Kostinek, M., Specht, I., Edward, V. A., Pinto, C., Egounlety, M., Sossa, C., Mbugua, S.,
650 Dortu, C., Thonart, P., Taljaard, L., Mengu, M., Franz, C. M., & Holzapfel, W. H. (2007).
651 Characterisation and biochemical properties of predominant lactic acid bacteria from
652 fermenting cassava for selection as starter cultures. *International Journal of Food*
653 *Microbiology*, 114, 342-351.

654

655 Kroghsbo, S., Rigby, N.M., Johnson, P.E., Adel-Patient, K., Bogh, K.L., Salt, L. J., Mills,
656 E.N., & Madsen, C. B. (2014). Assessment of the sensitizing potential of processed peanut
657 proteins in Brown Norway rats: roasting does not enhance allergenicity. *PLoS ONE*, 9, 96475.

658

659 Ladero, V., Calles-Enriquez, M., Fernandez, M., & Alvarez, M. A. (2010). Toxicological
660 effects of dietary biogenic amines. *Current Nutrition and Food Sciences*, 6, 145–156.

661

662 Lahtinen, S. J., Haskard, C. A., Ouwehand, A. C., Salminen, S. J., & Ahokas J. T. (2004).
663 Binding of aflatoxin B1 to cell wall components of *Lactobacillus rhamnosus* strain GG. *Food*
664 *Additive and Contaminants*, 21, 158-164.

665

666 Lai, L. R., Hsieh, S. C., Huang, H. Y., & Chou, C. C. (2013). Effect of lactic fermentation on
667 the total phenolic, saponin and phytic acid contents as well as anti-colon cancer cell
668 proliferation activity of soymilk. *Journal of Bioscience and Bioengineering*, 115, 552-556.

669

670 Lee, Y. C., Kung, H. F., Huang, Y. L., Wu, C. H., Huang, Y. R., & Tsai, Y. H. (2016).
671 Reduction of biogenic amines during miso fermentation by *Lactobacillus plantarum* as a
672 starter culture. *Journal of Food Protection*, 79(9):1556-1561.

673

674 Long, M., Li, P., Zhang, W., Li, X., Zhang, Y., Wang, Z., & Liu, G. (2012). Removal of
675 zearalenone by strains of *Lactobacillus* sp. isolated from rumen *in vitro*. *Journal of Animal*
676 *and Veterinary Advances*, 11, 2417-2422.

677

678 Lopez, H. W., Ouvry, A., Bervas, E., Guy, C., Messenger, A., Demigne, C., & Remesy, C.
679 (2000). Strains of lactic acid bacteria isolated from sour doughs degrade phytic acid and
680 improve calcium and magnesium solubility from whole wheat flour. *Journal of Agricultural*
681 *and Food Chemistry*, 48, 2281-2285.

682

683 Lucas, P. M., Wolken, W. A. M., Claisse, O., Lolkema, J. S., & Lonvaud-Funel, A. (2005).
684 Histamine-producing pathway encoded on an unstable plasmid in *Lactobacillus hilgardii*
685 0006. *Applied and Environmental Microbiology*, 71, 1417-1424.

686

687 Maenz, D. D., Engele-Schaan, C. M., Newkirk, R. W., & Classen, H. L. (1999). The effect of
688 minerals and mineral chelators on the formation of phytase-resistant and phytase-susceptible
689 forms of phytic acid in solution and in a slurry of canola meal. *Animal Feed Science and*
690 *Technology*, 81, 177-192.

691

692 Mah, J. H., Park, Y. K., Jin, Y. H., Lee, J. H., & Hwang, H. J. (2019). Bacterial production
693 and control of biogenic amines in asian fermented soybean foods. *Foods*, 8, 85.

694

695 Martín-Sánchez, A. M., Chaves-López, C., Sendra, E., Sayas, E., Fernández-López, J., &
696 Pérez-Álvarez, J. Á. (2011). Lipolysis, proteolysis and sensory characteristics of a Spanish

697 fermented dry-cured meat product (salchichón) with oregano essential oil used as surface
698 mold inhibitor. *Meat Science*, 89, 35-44.

699

700 Mills, E. N. C., Sancho, A. I., Rigby, N. M., Jenkins, J. A., Mackie, A. R. (2009). Impact of
701 food processing on the structure and allergenic properties of food allergens. *Molecular*
702 *Nutrition & Food Research*, 53, 963–969.

703

704 Motarjemi, Y., & Nout, M. J. (1996). Food fermentation: a safety and nutritional assessment.
705 Joint FAO/WHO Workshop on Assessment of Fermentation as a Household Technology for
706 Improving Food Safety. *Bulletin of the World Health Organization*, 74(6), 553.

707

708 Nazzaro, F., Fratianni, F., Coppola, R., & Feo, V. D. (2017). Essential oils and antifungal
709 activity. *Pharmaceuticals* (Basel, Switzerland), 10, 86.

710

711 Nguyen, H., Elegado, F. B., Librojo-Basilio, N. T., Mabesa, R. C., & Dizon, E. I. (2009).
712 Isolation and characterisation of selected lactic acid bacteria for improved processing of Nem
713 chua, a traditional fermented meat from Vietnam. *Beneficial Microbes*, 1, 67-74.

714

715 Niderkorn, V., Morgavi, D. P., Aboab, B., Lemaire, M., & Boudra, V. (2009). Cell wall
716 component and mycotoxin moieties involved in the binding of fumonisin B1 and B2 by lactic
717 acid bacteria. *Journal of Applied Microbiology*, 106, 977-985.

718

719 Nowak-Wegrzyn, A., & Fiocchi, A. (2009). Rare, medium, or well done? The effect of
720 heating and food matrix on food protein allergenicity. *Current Opinion in Allergy and*
721 *Clinical Immunology*, 9, 234–237.

722

723 Osawa, R., Kuroiso, K., Goto, S., & Shimizu, A. (2000). Isolation of tannin-degrading
724 lactobacilli from humans and fermented foods. *Applied and Environmental Microbiology*, 66,
725 3093-3097.

726

727 Palacios, M. C., Haros, M., Rosell, C. M., & Sanz, Y. (2005). Characterization of an acid
728 phosphatase from *Lactobacillus pentosus*: regulation and biochemical properties. *Journal of*
729 *Applied Microbiology*, 98, 229-237.

730

731 Parada, J. L., Caron, C. R., Medeiros, A. B. P., & Soccol, C. R. (2007). Bacteriocins from
732 lactic acid bacteria: purification, properties and use as biopreservatives. *Brazilian Archives of*
733 *Biology and Technology*, 50, 512-542.

734

735 Park, Y. K., Lee, J. H., & Mah, J. H. (2019). Occurrence and reduction of biogenic amines in
736 traditional Asian fermented soybean foods: A review. *Food Chemistry*, 278, 1–9.

737

738 Phan, T. T., Phạm, C. T., & Phạm, T. H. (2006). Nghiên cứu ứng dụng các chế phẩm từ tòi
739 trong công nghệ sản xuất nem chua nhằm nâng cao chất lượng và kéo dài thời gian bảo quản.
740 Tuyển tập Hội nghị khoa học lần thứ 20, kỷ niệm 50 năm thành lập Trường ĐHBK Hà Nội,
741 224-229.

742

743 Phan, Y. T. N., Tang, M. T., Tran, T. T. M., Nguyen, V. H., Nguyen, T. H., Tsuruta, T., &
744 Nishino, N. (2017). Diversity of lactic acid bacteria in vegetable-based and meat-based
745 fermented foods produced in the central region of Vietnam. *AIMS Microbiology*, 3, 61-70.

746

747 Pranoto, Y., Anggrahini, S., & Efendi, Z. (2013). Effect of natural and *Lactobacillus*
748 *plantarum* fermentation on *in vitro* protein and starch digestibilities of sorghum flours. *Food*
749 *Bioscience*, 2, 46–52.

750

751 Pranoto, Y., Rakshit, S. K., & Salokhe, V. M. (2005). Enhancing antimicrobial activity of
752 chitosan films by incorporating garlic oil, potassium sorbate and nisin. *LWT - Food Science*
753 *and Technology*, 38, 859-865.

754

755 Raghavendra, P., & Halami, P. M. (2009). Screening, selection and characterization of phytic
756 acid degrading lactic acid bacteria from chicken intestine. *International Journal of Food*
757 *Microbiology*, 133, 129-134.

758

759 Raghavendra, P., Ushakumari, S., & Halami, P. (2011). Phytate-degrading *Pediococcus*
760 *pentosaceus* CFR R123 for application in functional foods. *Beneficial Microbes*, 2, 57-61.

761

762 Rahaman, T., Vasiljevic, T., & Ramchandran, L. (2016). Effect of processing on
763 conformational changes of food proteins related to allergenicity. *Trends in Food Science &*
764 *Technology*, 49, 24-34.

765

766 Reale, A., Konietzny, U., Coppola, R., Sorrentino, E., & Greiner, R. (2007). The importance
767 of lactic acid bacteria for phytate degradation during cereal dough fermentation. *Journal of*
768 *Agricultural and Food Chemistry*, 55, 2993-2997.

769

770 Reddy, N. R., & Salunkhe, D. K. (1980). Effects of fermentation on phytate phosphorus and
771 mineral content in black gram, rice, and black gram and rice blends. *Journal of Food Science*,
772 45, 1708-1712.

773

774 Reverón, I., Jiménez, N., Curiel, J. A., Peñas, E., de Felipe, F. L., de las Rivas, B., & Muñoz,
775 R. (2017). Differential gene expression by *Lactobacillus plantarum* WCFS1 in response to
776 phenolic compounds reveals new genes involved in tannin degradation. *Applied and*
777 *Environmental Microbiology*, 83, e03387-16.

778

779 Richter, E. D., & Chlamtac, N. (2002). Ames, Pesticides, and Cancer Revisited. *International*
780 *Journal of Occupational and Environmental Health*, 8, 63-72.

781

782 Rodríguez, H., Curiel, J. A., Landete, J. M., de las Rivas, B., López de Felipe, F., Gómez-
783 Cordovés, C., Mancheño, J. M., & Muñoz, R. (2009). Food phenolics and lactic acid bacteria.
784 *International Journal of Food Microbiology*, 132, 79-90.

785

786 Rodríguez, H., de las Rivas, B., Gómez-Cordovés, C., & Muñoz, R. (2008). Characterization
787 of tannase activity in cell-free extracts of *Lactobacillus plantarum* CECT 748 T. *International*
788 *Journal of Food Microbiology*, 121, 92-98.

789

790 Satomi, M., Furushita, M., Oikawa, H., Yoshikawa-Takahashi, M., & Yano, Y. (2008).
791 Analysis of a 30 kbp plasmid encoding histidine decarboxylase gene in *Tetragenococcus*
792 *halophilus* isolated from fish sauce. *International Journal of Food Microbiology*, 126, 202–
793 209.

794

795 Savard, T., Beaulieu, C., Boucher, I., & Champagne, C. P. (2002). Antimicrobial action of
796 hydrolyzed chitosan against spoilage yeasts and lactic acid bacteria of fermented vegetables.
797 *Journal of food Protection*, 65, 828-833.

798

799 Shalaby, A. R. (2000). Changes in biogenic amines in mature and germinating legume seeds
800 and their behavior during cooking. *Nahrung/Food*, 44, 23-7.

801

802 Shin, K.-H., Lim, Y., Ahn, J. H., Khil, J., Cha, C. J., & Hur, H. G. (2005). Anaerobic
803 biotransformation of dinitrotoluene isomers by *Lactococcus lactis* subsp. *lactis* strain 27
804 isolated from earthworm intestine. *Chemosphere*, 61, 30-39.

805

806 Shirai, K., Revah-Moiseev, S., García-Garibay, M., & Marshall, V. M. (1994). Ability of
807 some strains of lactic acid bacteria to degrade phytic acid. *Letters in Applied Microbiology*,
808 19, 366-369.

809

810 Siedler, S., Balti, R., & Neves, A. R. (2019). Bioprotective mechanisms of lactic acid bacteria
811 against fungal spoilage of food. *Current Opinion in Biotechnology*, 56, 138-146.

812

813 Sindhu, S. C., & Khetarpaul, N. (2001). Probiotic fermentation of indigenous food mixture:
814 effect on antinutrients and digestibility of starch and protein. *Journal of Food Composition*
815 *and Analysis*, 14, 601-609.

816

817 Song, Y. S., Frias, J., Martinez-Villaluenga, C., Vidal-Valdeverde, C., & Gonzalez de Mejia,
818 E. (2008a). Immunoreactivity reduction of soybean meal by fermentation, effect on amino

819 acid composition and antigenicity of commercial soy products. *Food Chemistry*, 108, 571-
820 581.

821

822 Song, Y. S., Martinez-Villaluenga, C., & Gonzalez de Mejia, E. (2008b). Quantification of
823 human IgE immunoreactive soybean proteins in commercial soy ingredients and products.
824 *Journal of Food Science*, 73, 90-99.

825

826 Songré-Ouattara, L. T., Mouquet-Rivier, C., Icard-Vernière, C., Humblot, C., Diawara, B., &
827 Guyot, J. P. (2008). Enzyme activities of lactic acid bacteria from a pearl millet fermented
828 gruel (ben-saalga) of functional interest in nutrition. *International Journal of Food*
829 *Microbiology*, 128, 395-400.

830

831 Sreeramulu, G., Srinivasa, D. S., Nand, K., & Joseph, R. (1996). *Lactobacillus amylovorus* as
832 a phytase producer in submerged culture. *Letters in Applied Microbiology*, 23, 385-388.

833

834 Starzyńska-Janiszewska, A., Stodolak, B., & Mickowska, B. (2014). Effect of controlled
835 lactic acid fermentation on selected bioactive and nutritional parameters of tempeh obtained
836 from unhulled common bean (*Phaseolus vulgaris*) seeds. *Journal of the Science of Food and*
837 *Agriculture*, 94, 359-366.

838

839 Svensson, L., Sekwati-Monang, B., Lutz, D. L., Schieber, A., & Gänzle, M. G. (2010).
840 Phenolic acids and flavonoids in nonfermented and fermented red sorghum (*Sorghum bicolor*
841 (L.) Moench). *Journal of Agricultural and Food Chemistry*, 58, 9214-9220.

842

843 Taheur, F. B., Fedhila, K., Chaieb, K., Kouidhi, B., Bakhrouf, A., & Abrunhosa, L. (2017).
844 Adsorption of aflatoxin B1, zearalenone and ochratoxin A by microorganisms isolated from
845 Kefir grains. *International Journal of Food Microbiology*, 251, 1–7.

846

847 Takahashi-Ando, N., Ohsato, S., Shibata, T., Hamamoto, H., Yamaguchi, I., & Kimura, M.
848 (2004). Metabolism of zearalenone by gene tically modified organisms expressing the
849 detoxification gene from *Clonostachys rosea*. *Applied Environmental Microbiology*, 70,
850 3239–3245.

851

852 Tamang, J. P., Shin, D. H., Jung, S. J., & Chae, S. W. (2016). Functional properties of
853 microorganisms in fermented foods. *Frontiers in Microbiology*, 7, 578.

854

855 Tamayo-Ramos, J. A., Sanz-Penella, J. M., Yebra, M. J., Monedero, V., Haros, M., 2012.
856 Novel phytases from *Bifidobacterium pseudocatenulatum* ATCC 27919 and *Bifidobacterium*
857 *longum* subsp. *infantis* ATCC 15697. *Applied and Environmental Microbiology*, 78, 5013–
858 5015.

859

860 Tang, A. L., Wilcox, G., Walker, K. Z., Shah, N. P., Ashton, J. F., & Stojanovska, L. (2010).
861 Phytase activity from *Lactobacillus* spp. in calcium-fortified soymilk. *Journal of Food*
862 *Science*, 75, M373-376.

863

864 Tsatsakis, A. M., Nawaz, M. A., Tutelyan, V. A., Golokhvast, K. S., Kalantzi, O. I., Chung,
865 D. H., Kang, S. J., Coleman, M. D., Tyshko, N., Yang, S. H., & Chung, G. (2017). Impact on
866 environment, ecosystem, diversity and health from culturing and using GMOs as feed and
867 food. *Food and Chemical Toxicology*, 107, 108-121.

868

869 Tubiello, F. N. (2018). Greenhouse gas emissions due to agriculture. *Encyclopedia Food*
870 *Security Sustainability*, 1, 196–205.

871

872 Untersmayr, E., & Jensen-Jarolim, E. (2008). The role of protein digestibility and antacids on
873 food allergy outcomes. *Journal of Allergy and Clinical Immunology*, 121, 1301-1308.

874

875 Vaquero, I., Marcobal, Á., & Muñoz, R. (2004). Tannase activity by lactic acid bacteria
876 isolated from grape must and wine. *International journal of food microbiology*, 96, 199-204.

877

878 Vekiru, E., Hametner, C., Mitterbauer, R., Rechthaler, J., Adam, G., Schatzmayr, G., Krska,
879 R., & Schuhmacher, R. (2010). Cleavage of zearalenone by *Trichosporon mycotoxinivorans*
880 to a novel nonestrogenic metabolite. *Applied and Environmental Microbiology*, 76, 2353–
881 2359.

882

883 Wang, L., Yue, T., Yuan, Y., Wang, Z., Ye, M., & Cai, R. (2015). A new insight into the
884 adsorption mechanism of patulin by the heat-inactive lactic acid bacteria cells. *Food*
885 *Control*, 50, 104-110.

886

887 Zamudio, M., González, A., & Medina, J. A. (2001). *Lactobacillus plantarum* phytase activity
888 is due to non-specific acid phosphatase. *Letters in Applied Microbiology*, 32, 181-184.

889

890 Zhan, H., Feng, Y., Fan, X., & Chen, S. (2018). Recent advances in glyphosate
891 biodegradation. *Applied Microbiology and Biotechnology*, 102, 5033-5043.

892

893 Zhang, Y.-H., Xu, D., Liu, J. Q., & Zhao, X. H. (2014). Enhanced degradation of five
894 organophosphorus pesticides in skimmed milk by lactic acid bacteria and its potential
895 relationship with phosphatase production. *Food Chemistry*, 164, 173-178.

896

897 Zhao, Z., Liu, N., Yang, L., Wang, J., Song, S., Nie, D., Yang, X., Hou, J., & Wu, A. (2015).
898 Cross-linked chitosan polymers as generic adsorbents for simultaneous adsorption of multiple
899 mycotoxins. *Food Control*, 57, 362-369.

900

901

