



Technologically relevant *Bacillus* species and microbial safety of West African traditional alkaline fermented seed condiments

James Owusu-Kwarteng , Charles Parkouda , Gbenga Adedeji Adewumi ,
Labia Irène Ivette Ouoba & Lene Jespersen

To cite this article: James Owusu-Kwarteng , Charles Parkouda , Gbenga Adedeji Adewumi ,
Labia Irène Ivette Ouoba & Lene Jespersen (2020): Technologically relevant *Bacillus* species and
microbial safety of West African traditional alkaline fermented seed condiments, Critical Reviews in
Food Science and Nutrition, DOI: [10.1080/10408398.2020.1830026](https://doi.org/10.1080/10408398.2020.1830026)

To link to this article: <https://doi.org/10.1080/10408398.2020.1830026>



Published online: 08 Oct 2020.



Submit your article to this journal [↗](#)



Article views: 35



View related articles [↗](#)




View Crossmark data [↗](#)

REVIEW



Technologically relevant *Bacillus* species and microbial safety of West African traditional alkaline fermented seed condiments

James Owusu-Kwarteng^a , Charles Parkouda^b, Gbenga Adedeji Adewumi^c, Labia Irène Ivette Ouoba^d, and Lene Jespersen^e

^aDepartment of Food Science and Technology, University of Energy and Natural Resources, Sunyani, Ghana; ^bCNRST/IRSAT/DTA, Centre National de la Recherche Scientifique et Technologique, Ouagadougou, Burkina Faso; ^cDepartment of Microbiology, Faculty of Science, University of Lagos, Lagos, Nigeria; ^dDepartment of Health and Human Sciences, Microbiology Research Unit, London Metropolitan University, London, UK; ^eDepartment of Food Science, Food Microbiology, University of Copenhagen, Copenhagen, Denmark

ABSTRACT

Fermented food condiments serve as a major source of nutrients to many homes in West Africa, especially among the rural poor who use these condiments as a cheap source of protein substitute for milk and other animal protein sources. Traditional fermented West African condiments are produced by spontaneous fermentation of legumes and protein-rich seeds of both cultivated and wild plant species. These fermented condiments are culturally accepted and widely produced in the West African sub-region, and rely on indigenous microbiota responsible for taste, texture, aroma development and the overall unique product characteristics. Detailed understanding of fermentation microbiota and their unique technological and functional properties are fundamental in developing products with enhanced quality and safety, as well as development of specific locally adapted starter cultures. Technologically relevant *Bacillus* spp., mainly *Bacillus subtilis*, are the predominant fermentative bacteria responsible for the natural fermentation of condiments across West Africa. Other species of *Bacillus* including *B. amyloliquefaciens*, *B. licheniformis*, *B. pumilus*, *B. megaterium*, *B. sphaericus*, *B. cereus*, *B.adius* and *B. fusiformis* are also frequently involved in the fermentation process. These bacterial species are responsible for flavor development, bio-conversion of complex food molecules, and production of antimicrobial compounds that impact shelf-life and safety, and in some instances, may confer host-beneficial health effects beyond basic nutrition. First, this review provides currently available information on the technologically relevant *Bacillus* species isolated from fermented food condiments in nine (9) West African countries. In addition, perspectives on harnessing the potentials of the technologically beneficial bacterial strains in fermented condiments in West Africa for enhanced food safety, quality and overall food security is presented.

KEYWORDS

Spontaneous fermentation; food safety; *Bacillus subtilis*; protein degradation; legume; West Africa

Traditional alkaline fermentation of seed condiments in West Africa

Protein-rich plant seeds are fermented into condiments in West Africa, and they constitute an important component of the peoples' diets. These condiments are popular across the West African sub-region for their sensory characteristics and high nutritional value, where they serve as flavoring in soups and stews, and form a significant source of low-cost protein in the predominantly starchy staple region (Azokpota, Hounhouigan, and Nago 2006; Dakwa et al. 2005; Parkouda et al. 2009). The raw materials for the processing of fermented condiments in West Africa come from many different plant species, including seeds of several wild trees, as well as various cultivated leguminous plants (Achi 2005; Ogunshe, Omotosho, and Ayansina 2007; Ouoba et al. 2004; Parkouda et al. 2009; Terlabie, Sakyi-Dawson, and Amoa-Awua 2006). Fermented condiments produced from the

same raw material with similar or minor differences in production process may be known by different local names depending on country or local region of production. For example, while *dawadawa* is a common name for spontaneously fermented African locust bean [*Parkia biglobosa* (Jacq. Benth)] in Ghana and Nigeria, the same product is also known under different local names such as *soumbala* in Burkina Faso (Ouoba et al. 2004), *afitin*, *iru* or *sonru* in Benin (Azokpota, Hounhouigan, and Nago 2006), *nététou* in Senegal (N'Dir et al. 1994), *kinda* in Sierra Leone and *iru* in some parts of Nigeria (Sanni et al. 2000). Similarly, fermented condiment from roselle seeds [*Hibiscus sabdariffa* (Linn.)] is known by different local names such as *bikalga* in Burkina Faso (Ouoba et al. 2008), *yanyanku* and *ikpiru* in Benin (Agbobatinkpo et al. 2013) and *mbuja* in Cameroon (Mohamadou, Mbofung, and Barbier 2013). Different plant species commonly used for the processing of various

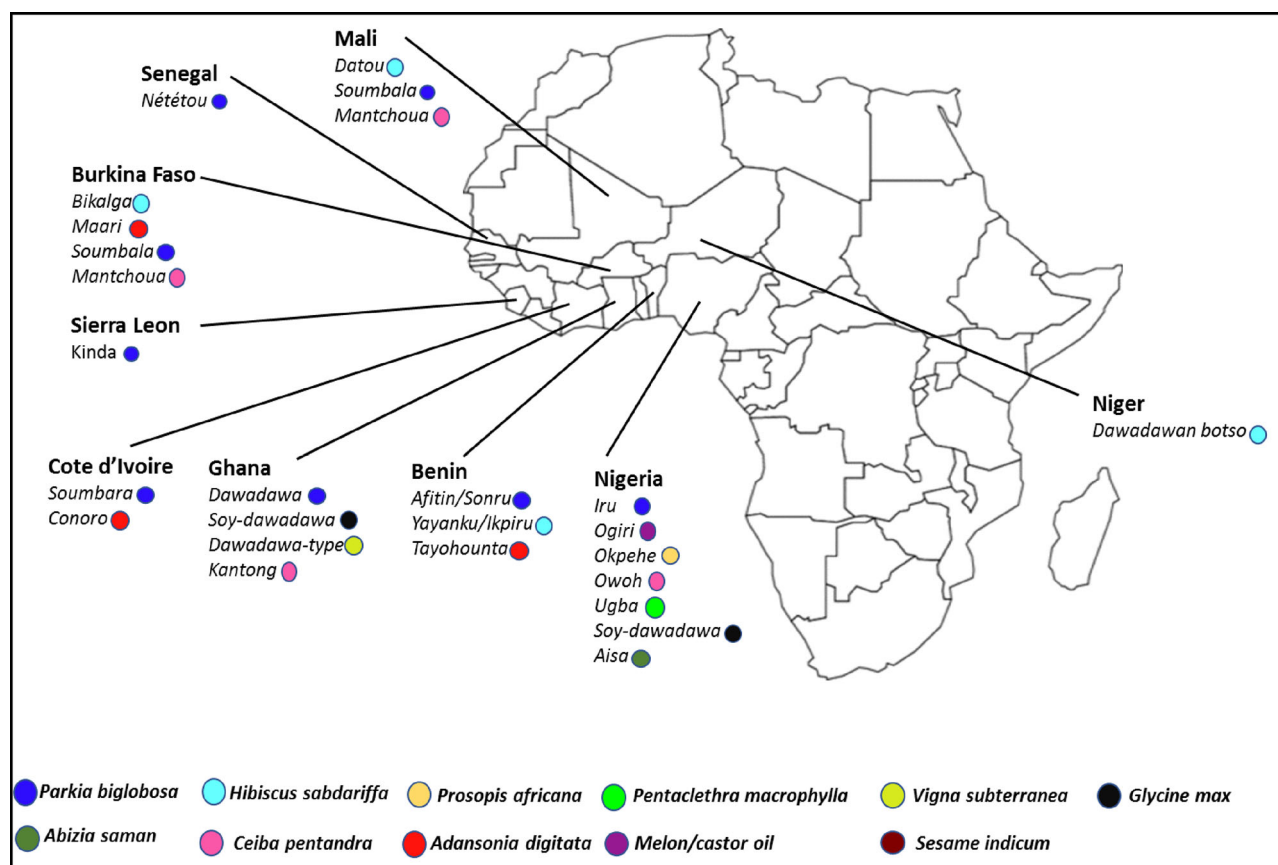


Figure 1. Common plant species for the processing of West African fermented seed condiments.

condiments in different West African countries is shown in Figure 1.

As a typical artisanal process, West African fermented seed condiments are produced at household or small-scale level, with most phases of the production process and parameters, such as pH, time, and temperature are often poorly controlled. The fermentative process, which is considered as a crucial phase in the production of fermented foods, is spontaneous or achieved by back-slopping, a process that affects product quality and safety. Consequently, a huge diversity of microorganisms has been detected, in association with the fermentation of West African traditional fermented seed condiments. Thus, it is possible to find a heterogeneous population of microbiota, including the technologically important, as well as microbial pathogens and/or strains liable to synthesize toxic by-products such as mycotoxins, ethyl carbamate and biogenic amines in the spontaneously fermented condiments with negative implications for food safety and public health.

Due to the proteinaceous nature of the plant raw materials used for the processing of food condiments, the natural fermentation of these raw materials is generally characterized by extensive hydrolysis of the proteins into peptides, amino acids and ammonia, resulting in pH increasing to about 8–10 in the final product (Aderibigbe and Odunfa 1990; Leejeerajumnean et al. 2001; Odunfa 1985; Omafuvbe et al. 2004). However, in a few fermented seed products such as *kantong* produced in northern Ghana, the addition of cassava flour to *Ceiba pentandra* (kapok) seeds leads to a

co-dominance of lactic acid bacteria (LAB) and *Bacillus* in the fermentation matrix resulting in relatively lower pH of about 5–7 (Kpikpi et al. 2010). Other important biochemical activities such as degradation of oligosaccharides to simple sugars have also been reported (Omafuvbe, Shonukan, and Abiose 2000; Ouoba, Diawara, Christensen, et al. 2007). Fermentation of protein-rich seeds into condiments in West Africa are reportedly dominated by aerobic endospore-forming bacteria (AEB), particularly *Bacillus* spp., with AEB counts reaching 10 Log₁₀ CFU/g in the final products (Kaboré et al. 2012; Parkouda et al. 2009; Parkouda et al. 2010). During the fermentation process, *Bacillus* spp. degrade plant proteins into peptides and amino acids (Odunfa, 1985; Ouoba et al., 2003). Subsequently, the free amino acids are utilized by the *Bacillus* as carbon and nitrogen sources, to produce ammonia/ammonium hydroxide, resulting in high pH values and the associated atypical odor of these fermented condiments (Amoa-Awua et al. 2014; Ouoba et al. 2005; Ouoba, Rechinger, et al. 2003; Parkouda et al. 2009). Furthermore, the microbiological and biochemical processes occurring during alkaline fermentation of seed condiments are reported to improve the nutritional value of the final products through transformation of the chemical constituents of the raw material. Degradation of anti-nutritive factors, improvements in digestibility and increase in concentrations of vitamins, minerals, and essential amino acids have also been reported for fermented seed condiments (Adams 1990; Kwak et al. 2010; Makanjuola and Ajayi 2012; Okechukwu et al. 2012; Parkouda et al. 2009).

Indeed, several studies have reported the contribution of fermented condiments to the nutritional requirements of consumers, where they serve as sources of essential amino acids and fatty acids, including B vitamins (Odunfa and Adesomoju 1985; Odunfa and Adesomoju 1986). High levels of free amino acids, non-protein and soluble nitrogenous compounds are reported in *iru*, a West African fermented seed condiment (Azokpota, Hounhouigan, and Nago 2006; Azokpota et al. 2006; Gernah, Inyang, and Ezeora 2007). Also, increase in the concentration of essential amino acids, particularly, methionine, phenylalanine, leucine, isoleucine and lysine during alkaline fermentation of African locust bean has been reported (Ouoba, Cantor, et al. 2003).

The microbiota of fermented condiments greatly influences product characteristics, such as quality, safety and products functionality. Despite the similarities that exist among the various condiments produced in West Africa, previous investigations have independently focused on the isolation, characterization and identification of dominant microorganisms involved in the fermentation of these products in different countries. Irrespective of raw material or country of production, most of these investigations, have reported the dominance of *Bacillus* spp. in these condiments (Adewumi et al. 2013; Agbobatinkpo et al. 2013; Amoa-Awua, Terlabie, and Sakyi-Dawson 2006; Azokpota et al. 2007; Meerak et al. 2008; Oguntuyinbo et al. 2010; Ouoba et al. 2008; Parkouda et al. 2009; Parkouda et al. 2010).

Information on the unique features including technological and functional properties of the fermentative *Bacillus* species isolated from fermented condiments in West Africa have been sparsely reported in literature. Thus, except for a previously published review on the microbiology of alkaline fermented condiments in Africa and Asia more than a decade ago (Parkouda et al. 2009), there is lack of a current comprehensive overview of the fermentative and technologically relevant *Bacillus* species in West African alkaline fermented food condiments. This information is however, fundamental to designing locally adapted common starter culture(s) that could contribute significantly to enhancing food safety, food quality and overall food and nutrition security in the sub-region. Therefore, the aim of this paper is to present a comprehensive review of the status of currently available knowledge on the fermentative and technologically relevant *Bacillus* species isolated from alkaline fermented seed condiments in West Africa. The information in this review is presented with a focus on the taxonomic diversity, distribution and interactions of *Bacillus* species in alkaline fermented seed condiments in West Africa. Additionally, technological and functional properties of *Bacillus* species, including development of aroma compounds, nutritional improvements and degradation of toxins and production of antimicrobial compounds are presented. Microbial safety aspects of West African alkaline fermented seed condiments as well as perspectives and innovations for future developments are proposed within the context of food quality, safety and overall food security in West Africa.

Taxonomic diversity and distribution of *Bacillus* spp. in fermented condiments

Conventionally, microbiological procedures of selective isolation, enumeration, taxonomical profiling and identification have been employed to analyze the microbiota of different indigenous fermented food condiments in West Africa. These classical techniques include cultural morphology, microscopic, biochemical or physiological characteristics and other phenotypic features such as carbohydrate fermentation profiles that are used in the detection, identification and differentiation of bacterial species associated with various African fermented foods (Obadina et al. 2008; Odunfa and Adesomoju 1985; Sanni, Ahrne, and Onilude 1995; Uzeh, Ohenhen, and Rojgubokan 2006). Microbial examinations of fermented food condiments in West Africa have been studied using traditional culturing and isolation approaches that are discriminatorily low, non-reproducible and laborious (Jeff-Agboola 2007; Okorie and Olasupo 2013a). Other challenges associated with these techniques include time consuming, and often times, ambiguous identifications (Rantsiou and Cocolin 2006). In a pioneer study by Odunfa (1981), colony morphology, microscopic examination, including cultural and biochemical characterization were used to identify the microorganisms associated with *iru*. Similarly, bacterial isolates in *dawadawa* and *daddawa*, using cultural characteristics and biochemical tests (Antai and Ibrahim 1986; Ogbadu and Okagbue 1988). The microorganisms associated with natural fermentation of mesquite seeds [*Prosopis africana* (Tuab)] for the production of *okpiye/okpehe* were also determined by microscopic parameters, cultural morphology and sugar fermentation profiles (Achi 1992). Also, *Bacillus* species involved in the fermentation of African oil bean [*Pentaclethra macrophylla* (Benth.)] seeds during *ugba* production were phenotypically characterized by employing physiological, microscopic and growth characteristics (Isu and Njoku 1997; Sanni et al. 2002). However, the availability of diverse culture-dependent molecular typing methods and culture-independent molecular assessment technologies, based on analysis of DNA or RNA used in recent years, has enabled better comprehension and more detailed understanding of the microbial composition and quantification, taxonomic identification, biodiversity and distribution of these fermented food condiments. An overview of predominant *Bacillus* species isolated from alkaline fermented seed condiments in West Africa is presented in Table 1.

Oguntuyinbo et al. (2010) used a combination of amplified ribosomal DNA restriction analysis (ARDRA) and randomly amplified polymorphic DNA (RAPD) PCR fingerprinting techniques to successfully differentiate between *Bacillus* species isolated from *okpehe*, a traditional fermented soup condiment from Nigeria. These authors, however, found that ARDRA digestion with *Hha*I, *Hinf*I and *Sau*3AI alone was not sufficient to differentiate between the *Bacillus* species; except for distinguishing *B. cereus* from *B. subtilis*. Subsequently, a simple, rapid, reproducible and reliable ARDRA protocol, based on *Rsa*I and *Cfo*I, which clearly differentiated closely related species of the *B. subtilis* sensu

Table 1. Overview of predominant *Bacillus* species occurring in fermented seed condiments in West Africa.

Product name	Substrate/raw material	<i>Bacillus</i> spp.	Method of identification	Country/region	Reference
Dawadawa	<i>Parkia biglobosa</i> seed	<i>B. subtilis</i> , <i>B. pumilus</i> , <i>B. licheniformis</i> , <i>B. firmus</i> , <i>B. atrophaeus</i> , <i>B. amyloliquefaciens</i> , <i>B. mojavensis</i> , <i>Lysinibacillus sphaericus</i> .	Phenotypic tests, 16S rRNA gene sequencing	Ghana	Amua-Awua et al. 2006; Meerak et al. 2008;
Dawadawa-type condiment	Bambara groundnut	<i>B. subtilis</i> subsp. <i>subtilis</i> , <i>B. amyloliquefaciens</i> subsp. <i>plantarum</i> , <i>B. pumilus</i> and <i>B. licheniformis</i>	MALDI-TOF MS, 16S rRNA and <i>gyrA</i> genes sequencing	Ghana	Akanni et al. 2018
Bikalga	<i>Hibiscus sabdariffa</i>	<i>B. subtilis</i> , <i>B. licheniformis</i> , <i>B. cereus</i> , <i>B. pumilus</i> , <i>B.adius</i> , <i>Brevibacillus borstelensis</i> , <i>B. sphaericus</i> , <i>B. fusiformis</i>	Phenotypic tests, 16S-23S rRNA (ITS-PCR) gene sequencing	Burkina Faso	Bengaly 2001; Ouoba et al. 2008
Iru	<i>Parkia biglobosa</i> seed	<i>B. subtilis</i> , <i>B. amyloliquefaciens</i> , <i>B. cereus</i> , <i>B. licheniformis</i> , <i>B. pumilus</i> and <i>Brevibacillus formosus</i>	Phenotypic tests, ARDRA, ITS-PCR, ITS-PCR-RFLP, RAPD-PCR, PCR-DGGE, 16S rRNA gene sequencing	Nigeria	Adewumi et al. 2013; Adewumi et al. 2014
Tayohounta	Baobab seed	<i>B. licheniformis</i> , <i>B. pumilus</i> , <i>B. subtilis</i> , <i>B. thermoamylovorans</i>	PCR-DGGE and cloning of 16s rRNA PCR fragments	Benin	Chadare et al. 2011
Ogiri	Melon/Castor oil seeds	<i>B. safensis</i> , <i>B. siamensis</i> , <i>B. altitudinis</i> , <i>B. encimensis</i>	Phenotypic tests, 16S rRNA gene sequencing	Nigeria	Adeyemi et al. 2018; Odunfa 1985
Okpehe	<i>Prosopis africana</i> seeds	<i>B. subtilis</i> , <i>B. amyloliquefaciens</i> , <i>B. cereus</i> , <i>B. licheniformis</i>	Phenotyping, RAPD-PCR, ARDRA fingerprinting, 16S rRNA gene sequencing	Nigeria	Oguntoyinbo et al. 2010
Soumbala	<i>Parkia biglobosa</i> seed	<i>B. subtilis</i> , <i>B. pumilus</i> , <i>B. cereus</i> , <i>B. sphaericus</i> , <i>Brevibacillus borstelensis</i> , <i>B. thuringiensis</i> , <i>B. licheniformis</i> , <i>B.adius</i> , <i>Paenibacillus alvei</i> , <i>B. firmus</i> , <i>P. larvae</i> , <i>Brevibacillus laterosporus</i> , <i>B. megaterium</i> , <i>B. mycoides</i>	ITS-PCR, ITS-PCR RFLP, PFGE, 16S rRNA sequencing, RAPD-PCR fingerprint	Burkina Faso	Ouoba et al. 2004; Sarkar et al. 2002
Ugba	<i>Pentaclethra macrophylla</i>	<i>B. cereus sensu lato</i> , <i>Lysinibacillus xylanilyticus</i> , <i>B. clausii</i> , <i>B. licheniformis</i> , <i>B. subtilis</i> and <i>B. safensis</i>	Phenotyping, sequencing of 16S rRNA, <i>gyrB</i> and <i>rpoB</i> genes, 16S-23S rRNA ITS-PCR and rep-PCR	Nigeria	Ahaotu et al. 2013
Afitin, sonru and iru	<i>Parkia biglobosa</i> seed	<i>B. subtilis</i> , <i>B. licheniformis</i> , <i>B. cereus</i> ,	ITS-PCR-RFLP, 16S rRNA gene sequencing	Benin	Azokpota et al. 2007
Nététou	<i>Parkia biglobosa</i> seed	<i>B. licheniformis</i> , <i>B. coagulans</i> , <i>B. subtilis</i> , <i>B. pumilus</i>	Phenotypic tests	Senegal	N'dir et al. 1994; N'dir et al. 1997
Soy-daddawa	Soybean	<i>B. subtilis</i>	Phenotypic, PCR-DGGE and 16S rRNA gene sequencing	Nigeria	Ezeokoli et al. 2016
Owoh	cotton seeds (<i>Gossypium hirsutum</i>)	<i>B. subtilis</i> , <i>B. licheniformis</i> , <i>B. pumilus</i> ,	Phenotypic tests	Nigeria	Sanni and Ogbonna 1991; Ezekiel et al. 2015
Maari	Baobab seed	<i>B. subtilis</i> , <i>B. licheniformis</i> , <i>B. velezensis</i> , <i>B. safensis</i> , <i>B. megaterium</i> , <i>B. endophyticus</i> , <i>B. cereus</i> , <i>B. coagulans</i> , <i>B. circulans</i>	Phenotypic tests, rep-PCR (GTG) ₅ -fingerprinting and 16S rRNA gene sequencing	Burkina Faso	Parkouda et al. 2010
Soumbara	<i>Parkia biglobosa</i> seed	<i>B. subtilis</i> , <i>B. velezensis</i> , <i>B. pumilis</i> ,	16S rRNA genes sequencing, RFLP analysis	Côte d'Ivoire	Adjoumani et al. 2019
Mbuja	<i>Hibiscus sabdariffa</i>	<i>B. subtilis</i> , <i>B. megaterium</i> , <i>B. amyloliquefaciens</i> , <i>B. pumilus</i> and <i>B. cereus</i>	Phenotypic tests, 16S rRNA and <i>gyrB</i> genes sequencing	Cameroon	Mohamadou et al. 2013
Yanyanku	<i>Hibiscus sabdariffa</i>	<i>B. subtilis</i> , <i>B. cereus</i> , <i>B. amyloliquefaciens</i> , <i>B. licheniformis</i> , <i>B. safensis</i> , <i>B. altitudinis</i> , <i>B. aryabhattai</i> , <i>B. flexus</i> , <i>B. circulans</i>	Phenotypic tests, rep-PCR, M13-PCR, 16S rRNA, <i>gyrA</i> , <i>gyrB</i> sequencing	Benin	Agbobatinkpo et al. 2013
Ikpiru	<i>Hibiscus sabdariffa</i>	<i>B. subtilis</i> , <i>B. cereus</i> , <i>B. amyloliquefaciens</i> , <i>B. licheniformis</i> , <i>B. safensis</i> , <i>B. altitudinis</i> , <i>B. aryabhattai</i> , <i>B. flexus</i> , <i>B. circulans</i>	Phenotypic tests, rep-PCR, M13-PCR, 16S rRNA, <i>gyrA</i> and <i>gyrB</i> genes sequencing	Benin	Agbobatinkpo et al. 2013
kantong	Kapok tree (<i>Ceiba pentandra</i>)	<i>B. subtilis</i> subsp. <i>subtilis</i> , <i>B. safensis</i> , <i>B. amyloliquefaciens</i> subsp. <i>plantarum</i>	Phenotypic tests, M13-PCR typing, 16S rRNA and <i>gyrA</i> genes sequencing	Ghana	KpiKpi et al., 2014

lato group present in *iru*, in particular, *B. licheniformis* from *B. subtilis* was developed (Adewumi et al. 2014; Jeyaram et al. 2011). Ouoba et al. (2004) genotypically characterized the interspecies and intraspecies relationship among *B. subtilis* and *B. pumilus* potential starter strains obtained from *soumbala* in Burkina Faso, using ITS-PCR, ITS-PCR-RFLP and PFGE. Similarly, ITS-PCR reportedly brought about interspecies differentiation among the *B. subtilis* group in *iru*, while ITS-PCR-RFLP with *CfoI* confirmed intraspecies variation, aside differentiating *B. pumilus* from *B. amyloliquefaciens*, which hitherto was a difficult task (Adewumi et al. 2014). Further RAPD-PCR analyses with OPA 18 and M13 primers revealed high strain level diversity among the dominant *B. subtilis* and *B. amyloliquefaciens* strains in *iru*, and these were completely diverged and phylogenetically different from *Bacillus* strains found in similar fermented food condiments in Asia (Adewumi et al. 2019; Adewumi et al. 2014). Repetitive-PCR and ITS-PCR were also used to distinguish *Bacillus* species from *bikalga*, and their identities confirmed by *gyrB* gene sequencing (Compaoré, Nielsen, Sawadogo-Lingani, et al. 2013; Ouoba et al. 2008). The *B. cereus* phylogeny possessing high 16S rRNA gene sequence similarity in *iru* were better separated by applying MLSA of chromosomally encoded housekeeping genes; *B. cereus sensu stricto* was clearly differentiated from *B. thuringiensis* (Adewumi et al. 2014). Thorsen et al. (2010; 2015) also employed phylogenetic analysis of concatenated gene sequences, as well as PCR-amplifications of toxigenic and virulent genes to identify *B. cereus sensu stricto*, *B. cereus* biovar *anthracis* and other species of the *B. cereus* group isolated from *maari* and Beninese traditional fermented food condiments.

Bacillus species responsible for the fermentation of baobab seeds [*Adansonia digitata* (L.)] for *maari* production, a fermented food condiment from Burkina Faso were characterized and identified using rep-PCR fingerprinting and 16S rRNA gene sequencing respectively (Parkouda et al., 2010). *Bacillus* species isolated during fermentation of African oil beans [*Pentaclethra macrophylla* (Benth.)] for *ugba* production were identified by sequencing of 16S rRNA, *gyrB* and *rpoB* genes; species and strains diversity were also conducted using ITS-PCR and rep-PCR (Ahaotu et al. 2013). Phylogenetic analysis of 16S rRNA and *gyrB* genes were used to identify and evaluate the diversity of 26 *Bacillus* species isolated from 12 samples of *mbuja*. *B. subtilis* and other related species were found most abundant. Genetic and phenotypic strains variability was found that can contribute to selection of starter cultures for *mbuja* production (Mohamadou, Mbofung, and Barbier 2013). The diversity of aerobic endospore-forming bacteria (AEB) occurring in *yanyanku* and *ikpiru* produced by spontaneous fermentation of *Gossypium hirsutum* and *H. sabdariffa* seeds respectively, was studied using genetic fingerprinting markers, including rep-PCR, M13-PCR, 16S rRNA, *gyrA* and *gyrB* PCR genes amplification (Agbobatinkpo et al. 2013). Although *yanyanku* and *ikpiru* are not directly consumed as food condiments, they are used as 'enrichment inocula' or 'starter materials' for the fermentation of *P. biglobosa* seeds into

fermented condiments such as *iru* and *sonru* in Benin. The use of *yanyanku* or *ikpiru* as enrichment inocula is to reduce fermentation time, exert a softening effect and ensure consistency in quality of the final product (Agbobatinkpo et al. 2011; Agbobatinkpo et al. 2012). *Bacillus subtilis* is the dominant species involved in the spontaneous fermentation of seeds to produce *yanyanku* and *ikpiru*, followed by *B. cereus*, *B. amyloliquefaciens*, *B. licheniformis*, *B. safensis* and *B. altitudinis* (Agbobatinkpo et al. 2013). In other related studies, *Bacillus* species isolated from *dawadawa* were characterized and identified by (GTG)₅-rep-PCR fingerprinting, 16S rRNA and *gyrA* genes sequencing as belonging to *B. subtilis* subsp. *subtilis*, *B. amyloliquefaciens* subsp. *plantarum*, *B. pumilus* and *B. licheniformis* as distinct clusters (Akanni et al. 2018). Similarly, the OTU of 16S rRNA gene sequencing representing *Bacillus* species were found to dominate in *iru* and *ogiri* (melon seed [*Citrullus vulgaris*] fermented condiment in Nigeria) (Adedeji et al. 2017; Ademola et al. 2018).

So far, only a few studies have applied culture-independent molecular techniques to investigate the community microbiota, diversity, spatial distribution and taxonomic identities of West African alkaline fermented food condiments. In one of such studies, 16S rRNA gene sequences obtained from PCR-DGGE DNA bands identified *B. subtilis* as the consistent and main bacterial species present in *iru*, sampled among different retail markets and local manufacturers (Adewumi et al., 2013). *B. licheniformis* and *Brevibacillus parabrevis* were also found to be present in at least one sample of *iru*. Sequencing of 16S rRNA clones of PCR-DGGE of bacterial DNA in *tayohounta*, a fermented baobab flavoring food condiment in Benin, revealed the frequent presence of *B. licheniformis*, *B. pumilus*, *B. subtilis*, *B. thermoamylovorans* and *Lactobacillus fermentum* in all the samples analyzed (Chadare et al. 2011). Also, in *soy-daddawa*, a Nigerian fermented soybean condiment, PCR-DGGE analysis of 16S rRNA gene indicated *Bacillus* species as the dominant OTU, occurring throughout the fermentation of *soy-daddawa* (Ezeokoli, Gupta, Popoola, et al. 2016; Ezeokoli, Gupta, Mienie, et al. 2016). Recent advancement in high-throughput next generation sequencing (NGS) platforms, such as, illumina, pyrosequencing, Ion Torrent and ABI SOLiD has delivered an entirely new strategy, employing massively parallel approaches to produce millions of short DNA sequence reads in a single run. These deep sequencing techniques have facilitated better understanding of the microbial community structures, dynamics and kinetics in many ecosystems, including the ecology of fermented food products, compared to other culture-independent molecular methods (Humblot and Guyot 2009; Jung et al. 2011; Kim et al. 2011). While information is available on the metagenomic analysis, as well as Illumina and pyrosequencing analysis of bacterial communities and distribution in Asian fermented soybean food condiments such as *da-jiang*, *doenjang*, *cheonggukjang* and *dajiang-meju* (Chun et al. 2020; Jung et al. 2016; Nam, Yi, and Lim 2012; Xie et al. 2019; Zhang et al. 2018), there is dearth of reports on the application of these techniques in profiling the complex

community structure and microbiota succession of fermented protein seeds in West Africa.

Microbial interactions occurring in alkaline fermented condiments

Spontaneous fermentation of seeds in West Africa is generally accompanied with mixed population of AEB, particularly the genera *Bacillus*, *Brevibacillus*, *Paenibacillus* and *Lysinibacillus*. Other microorganisms that have been identified, along with the major *Bacillus* spp. dominating West African seed condiments fermentation include members of the genera *Staphylococcus*, *Micrococcus*, *Proteus*, *Pseudomonas*, *Brevibacterium*, *Aerococcus*, LAB, yeasts and molds (Dakwa et al. 2005; Jeff-Agboola 2007; Okorie and Olasupo 2013b; Ouoba et al. 2010). *Staphylococcus vitulinus* and *S. saprophyticus* detected and identified in *iru* for the first time, and perhaps in any ethnic African fermented flavoring condiment, based on PCR-DGGE analysis of 16S rRNA gene, as a culture-independent molecular approach, were among the major bacterial species in *iru*, where they represent about 63% of the bacterial population (Adewumi 2016; Adewumi et al. 2013). Indeed, staphylococci have been previously thought to be the second dominant bacterial flora after *Bacillus* species or co-dominant with bacilli in various indigenous African fermented condiments, using traditional culture-dependent techniques, involving phenotypic, biochemical and molecular characterization (Antai and Ibrahim 1986; Chadare et al. 2011; Jeyaram et al. 2011; N'dir et al. 1997; Obeta 1983; Odunfa 1981; Ogbonna, Sokari, and Achinewhu 2001; Ogunshe, Omotosho, and Ayansina 2007; Okorie and Olasupo 2013b; Parkouda et al. 2010). However, the roles of these microorganisms during legume seeds fermentation is poorly understood (Adewumi 2016). Ouoba et al. (2019) while investigating the heterogeneity of *Staphylococcus* species in alkaline fermented foods described them as part of the secondary microbiota after *Bacillus*. *S. arlettae*, *S. aureus*, *S. cohnii*, *S. epidermidis*, *S. gallinarum*, *S. haemolyticus*, *S. hominis*, *S. pasteurii*, *S. condimenti*, *S. piscifermentans*, *S. saprophyticus*, *S. sciuri*, *S. simulans* and *S. warneri* were found present.

A number of studies indicate the occurrence or co-dominance of LAB with *Bacillus* in West African fermented seed condiments, particularly, in products where cassava or cereal flour is added to the seed during fermentation. In these products, LAB ferment various carbohydrates in the flour leading to lower pH values (4.9–6.9) of the final product (Kpikpi et al. 2010). In these types of products, interactions between LAB and the dominant *Bacillus* species might be important for product quality characteristics and safety. For succession of microbial species involved in the alkaline fermentation of seed condiments, *Bacillus* species are often reported to dominate throughout the fermentation period while LAB are often detected at the later stages of the fermentation processes. During the fermentation of *dawadawa*, *Leuconostoc dextranicum* and *Leuconostoc mesenteroides* significantly appeared only after 24 h of fermentation, whereas *Bacillus* species were dominantly present throughout the 72-

h fermentation period (Antai and Ibrahim 1986). LAB such as *Enterococcus faecium*, *E. hirae*, *E. durans*, *E. casseliflavus*, *L. fermentum*, *L. agilis*, *Leuconostoc mesenteroides*, *L. dextranicus*, *Streptococcus equinus*, *Pediococcus acidilactici*, *P. pentosaceus* and *Weissella confusa* have been identified in West African fermented condiments, but whose roles are yet to be ascertained (Antai and Ibrahim 1986; Chadare et al. 2011; Diaz et al. 2019; Kpikpi et al. 2010; Ouoba et al. 2010; Parkouda et al. 2010). The most common form of microbial interactions investigated so far in alkaline fermented food condiments in West Africa is antagonism. A mixed culture laboratory-scale fermentation of *Prosopis africana* seeds for *okpehe* production, involving bacteriocin-producing starter *B. subtilis* BFE 5301 and non-bacteriocin-producing *B. subtilis* BFE 5372, produced *okpehe* with acceptable sensory features, in which growth of *B. cereus* was antagonized and undetected (Oguntoyinbo et al. 2007). Similarly, *B. amyloliquefaciens* ssp. *plantarum* strains A4, I8 and G3 demonstrated antimicrobial activities against *B. cereus* NVH391-98, by inhibiting it when co-inoculated in *H. sabdariffa* seeds-based medium (Compaoré, Nielsen, Sawadogo-Lingani, et al. 2013). The *B. amyloliquefaciens* ssp. *plantarum* strains exhibited broad-spectrum antifungal and antibacterial properties in vitro, being able to qualitatively produce inhibitory compounds like lipopeptides, iturin, fengycin, surfactin, difficidin, macrolactin, bacillaene and the dipeptide bacilysin. Three *B. subtilis* strains (B3, B122 and B222) isolated from *maari*, which tested positive for bacteriocin production, delayed the growth of *B. cereus* NVH391-98 when co-cultured in a medium containing 5% (w/w) baobab seeds (Kaboré et al. 2013). In a bacteria-mould interaction, *B. subtilis* and *B. pumilus* strains from *soumbala* caused aberrant spore germination of *Aspergillus ochraceus*, with about five to eight log reduction, in addition to growth inhibition of *Micrococcus luteus*, *S. aureus*, *B. cereus*, *E. faecium*, *Listeria monocytogenes*, *Escherichia coli*, *Salmonella typhimurium*, *Shigella dysenteriae* and *Yersinia enterocolitica* during co-inoculation fermentation of *P. biglobosa* for *soumbala* production (Ouoba, Diawara, Jespersen, et al. 2007).

It is evident from the preceding reports that spontaneous fermentation of seed condiments in West Africa involves a complex microbial community, and their proliferation, metabolic activity and their intra- and interspecies interactions greatly influence the quality of these fermented condiments. Although several interaction mechanisms such as production of bacteriocins and antagonism have been widely described for various fermented foods microbiota, there is dearth of information on more complex interaction mechanisms such as cell-to-cell communication via quorum sensing (QS) and their impact on quality of alkaline fermented seed condiments in West Africa. However, it has been shown that, in traditional alkaline food fermentations, AEB are able to interact and influence each other's behavior through cell-to-cell communication system referred to as quorum sensing (Gori et al. 2011; Moslehi-Jenabian, Gori, and Jespersen 2009; Qian et al. 2015). Quorum sensing is conducted through a communication system by small and diffuse molecules called auto-inducer molecules (AI) or cell-

to-cell signal molecules that aim at signaling (Bassler 2002; Bassler and Losick 2006). Auto-inducer molecules are produced within a specific growth stage under specific physiological conditions or environmental changes, only acting after reaching a certain peak of concentration (*Quorum*) and being identified by specific receptors (Bassler 2002; Williams et al. 2007; Winzer et al. 2002). Autoinducer-2 (AI-2), a QS signaling molecule, produced by AEB strains of *B. subtilis*, *B. cereus*, *B. altitudinis*, *B. amyloliquefaciens*, *B. licheniformis*, *B. aryabhattai*, *B. safensis*, *Lysinibacillus macroides* and *Paenibacillus polymyxa* isolated from West African fermented seed condiments has been investigated, providing evidence of a quorum sensing system in *Bacillus* spp. and *L. macroides* (Qian et al. 2015). The authors showed by phylogenetic analysis that *luxS* gene, involved in the synthesis of AI-2, is widespread and highly conserved in *Bacillus* species, and further attributed this observation to the metabolic function of LuxS enzyme in the activated methyl cycle in addition to AI-2 signaling in AEB. The *luxS* gene has also been identified in food-borne LAB (Di Cagno et al. 2009) as well as food-borne pathogens (Coughlan et al. 2016). In bacteria, auto-inducers have been associated with improvements in access to nutrients and environmental niches (Skandamis and Nychas 2012; Waters and Bassler 2005), and optimization of cellular ability for morphological modification such as the formation of biofilm, reproduction, and sporulation (Bassler 2002; Henke and Bassler 2004; Skandamis and Nychas 2012). Additionally, auto-inducers are associated with the generation of defence responses against competitive organisms, expression of virulence factors and adaptation mechanisms to survive in hostile environments that limit growth (Bassler 2002, Skandamis and Nychas 2012; Taga and Bassler 2003; Waters and Bassler 2005). In general, auto-inducers such as AI-2 and other peptides can be of great significance for the quality and safety of West African alkaline food condiments. However, detailed knowledge of AI activity of the AEB and other microbial species involved in the fermentation of these food products is pertinent to the development of new QS-based strategies for improving the quality and safety of alkaline fermented food condiments.

Technological roles of *Bacillus* spp. in fermented condiments in West Africa

Aroma and flavor development

In addition to serving as rich source of nutrients to consumers, fermented condiments are likewise used in West Africa for their characteristics pleasant flavor and aroma (Agbobatinkpo et al. 2019; Akanni et al. 2018; Azokpota et al. 2008; Ouoba et al. 2005; Owens et al. 1997). The flavor of these fermented condiments has mainly been attributed to various volatile compounds, produced through the metabolic activities of microorganisms during fermentation, or due to other processing conditions, such as roasting and boiling (Azokpota et al. 2008; Azokpota et al. 2010; Dakwa et al. 2005; Leejeerajumnean et al. 2001; Ouoba et al. 2005). The production of specific aroma compounds has been

linked to activities of different *Bacillus* spp. during fermentation of seed condiments. Several volatile compounds contributing to the aroma and flavor profiles of West African fermented seed condiments have been identified (Table 2).

Differences in volatile compound profiles were reported to rely on the variable ability of the microbial species to degrade the proteins, lipids and carbohydrates of African locust beans (Ouoba et al. 2005). Thus, the development of aroma and flavor are related to the ability of the divergent *Bacillus* strains to degrade the proteins, lipids and carbohydrates of the substrate, through a diversity of extracellular hydrolases, which can contribute to flavor and aroma, generating reactions such as Maillard reactions, oxidation of lipids, degradation of amino acids and sugars (Aderibigbe and Odunfa 1990; Beaumont 2002; Leejeerajumnean et al. 2001). Indeed, metabolic activities of *Bacillus* species can generate various precursors, such as amino acids, monosaccharides, ammonia that are converted to volatile compounds, such as pyrazines (Owens et al. 1997). Moreover, adequate lipolytic activity of *Bacillus* species leads to the liberation of free fatty acids, which are required for the development of desired aroma characteristics (Beaumont 2002; Odunfa and Adesomoju 1986).

Traditional West African condiments are characterized by distinctive umami taste and therefore are used as meat or fish substitute for foods flavoring. Along with the four basic tastes of sweet, sour, salty and bitter, umami taste becomes the widely accepted 5th basic form of taste (Zhang et al. 2017). The influence of fermentation microbiota such as *Bacillus* species on proteolysis, and peptide hydrolysis, and the metabolism of glutamate and arginine in West African fermented seed condiments has been reported (Table 2). Consequently, umami substances, including free amino acids, nucleotides, peptides, organic acids and their derivatives, are widely distributed in fermented seed condiments, contributing to the overall taste these food condiments including the meat-like sensation and enhanced flavor characteristics.

Bioconversion of plant components

Degradation of proteins and amino acids synthesis

Protein has been reported as one of the major components of the raw materials used to produce alkaline fermented condiments in West Africa (Achi, Anokwuru, and Ogbo 2007; Amoa-Awua et al. 2014; Parkouda et al. 2009). A study of the biochemical changes associated with alkaline fermentation reveals that proteolysis is the main metabolic activity, leading to an increase in free amino acids (FAA), such as lysine, an essential amino acid (Odunfa 1985; Wang and Fung 1996). Previous investigations have shown significant increase in protease activity during alkaline fermentation of seeds to produce condiments in West Africa (Odunfa 1985; Oguntinyinbo et al. 2007; Parkouda, Diawara, and Debrah 2014). *Bacillus* spp., the major fermentation microorganisms involved in alkaline fermented condiments, are the main producers of proteolytic enzymes. Proteolysis due to *Bacillus* spp. results in the production of peptides,

Table 2. Specific examples of technological properties displayed by *Bacillus* spp. in West African fermented seed condiments.

Technological property	<i>Bacillus</i> species	Product	Specific activity expressed by <i>Bacillus</i> spp.	Reference
Production of Aroma/ flavor compounds	<i>B. subtilis</i>	<i>Ugba</i>	Production of phosphonous dichloride (Cl ₂ HP), chloro (1,1-dimethylethyl) phosphinomethyl; hexylidencyclohexane; pentanoic acid, 10-undecenyl ester; 2,6-ditert-butyl-4 (2,3,4,5,6-pentafluorobenzyl) phenol	Nwokeleme and Ugwuanyi 2015
	<i>B. subtilis</i>	Soybean <i>dawadawa</i>	Several aliphatic ketones, acetic acid, two aliphatic esters, several pyrazines, 2-pentylfuran, dimethyl sulfide, 2-methoxyphenol and trimethyloxazole were produced in 18 h fermented beans but were absent, or present in much lower concentrations, in roasted or autoclaved cotyledons. 3-hydroxy-2-butanone (acetoin), 2,5-dimethylpyrazine and trimethylpyrazine produced in large amounts.	Owens et al. 1997
	<i>B. subtilis</i>	<i>Soumbala</i>	116 compounds including pyrazines, aldehydes, ketones, esters, alcohols, acids, alkanes, alkenes, amines, pyridines, benzenes, phenols, sulfurs, furans produced in a 48-h controlled fermentation.	Ouoba et al. 2005
	<i>B. subtilis</i> subsp. <i>subtilis</i>	Bambara groundnut <i>dawadawa</i>	Produced 27 compounds; at level of 2398 ng/g. High level of sulfur compounds (1110 ng/g) with methanethiol and dimethyl disulfide detected.	Akanni et al. 2018
	<i>B. amyloliquefaciens</i> subsp. <i>plantarum</i>	Bambara groundnut <i>dawadawa</i>	Produced 37 compounds; total level of 11,952 ng/g. Organic acids, notably acetic acid (3460 ng/g) and <i>n</i> -hexadecanoic acid (2160 ng/g) produced. Phenols (700 ng/g), Dimethyl trisulfide (70 ng/g), dimethyl disulfide (610 ng/g), aldehydes (470 ng/g) and ketones (150 ng/g) produced.	Akanni et al. 2018
	<i>B. cereus</i>	Bambara groundnut <i>dawadawa</i>	Produced mainly ketones (1380 ng/g) alcohols and 2,5-dimethyl pyrazine (30 ng/g).	Akanni et al. 2018
	<i>B. licheniformis</i>	Bambara groundnut <i>dawadawa</i>	Produced 58 compounds; total level 15,030 ng/g dominated by aldehydes, particularly hexanal (710 ng/g), and esters. trace amount (2 ng/g) of 2,5-dimethyl pyrazine was also detected.	Akanni et al. 2018
	<i>B. megaterium</i>		Production of 2,4,6-tritert-butyl-4-methyl-2,5-cyclohexadien-1-one; (4E)-2,3,3-trimethyl-4-nonene; (Z) cyclododecene, 1,10-decanediol (72 h of fermentation).	Nwokeleme and Ugwuanyi 2015
Degradation of protein and amino acids synthesis	<i>B. subtilis</i>	<i>Soumbala</i>	Strain dependent significant increase in total and essential free amino acids (FAA), including lysine.	Ouoba et al. 2003
	<i>B. subtilis</i>	Soya bean	Protein degradation during 48 h fermentation of soya bean results in release of peptides. <i>In vitro</i> digestibility increases from 29% up to 33–43% after fermentation for 48 h.	Kiers et al. 2000
	<i>B. subtilis</i> ,	<i>Afitin, iru</i> and <i>sonru</i>	Strain dependent protease activity	Azokpota et al. 2006
	<i>B. licheniformis</i>	<i>Afitin, iru</i> and <i>sonru</i>	Strain dependent protease activity	Azokpota et al. 2006
	<i>B. licheniformis</i>		Extracellular protease production of up to 18.4 U/ml at 48 h of growth. Protease stable over pH 5.0–11 and at 60 °C for 60 m.	Olajuyigbe and Ajele 2008
	<i>B. pumilus</i>	<i>Soumbala</i>	Strain dependent significant increase in total and essential free amino acids (FAA), including lysine	Ouoba et al. 2003
Degradation of carbohydrates	<i>B. subtilis</i>	<i>Soumbala</i>	Liquefaction of galactomannan gels, strong ability to degrade arabinogalactan, stachyose and raffinose after 48 h of fermentation, yielding melibiose, fructose and traces of galactose as residual sugars. Degraded up to 85% of stachyose and	Ouoba e al. 2007

(continued)

Table 2. Continued.

Technological property	Bacillus species	Product	Specific activity expressed by <i>Bacillus</i> spp.	Reference
Degradation of oils	<i>B. subtilis</i>	Soya beans	100% (complete degradation) raffinose, releasing melibiose, fructose and galactose.	Kiers et al. 2000
	<i>B. pumilus</i>	Soumbala	Carbohydrate degradation during 48 h fermentation of soya bean. <i>In vitro</i> digestibility increases from 29% up to 33–43% after 48 h of fermentation	Ouoba et al. 2007
	<i>B. subtilis</i>	Soumbala	Weak degradation of carbohydrates	Ouoba et al. 2003
	<i>B. pumilus</i>	Soumbala	Strain dependent degradation of tributyrin and African locust bean oil with significantly high esterase and lipolytic activities for selected strains	Ouoba et al. 2003
	<i>B. subtilis</i>	Afitin, iru and sonru	Strain dependent degradation of tributyrin and African locust bean oil with significantly high esterase and lipolytic activities for selected strains	Ouoba et al. 2003
	<i>B. licheniformis</i>	Afitin, iru and sonru	High esterase activity (degradation of tributyrin) displayed by strains	Azokpota et al. 2006
Production of antimicrobial peptides	<i>B. subtilis</i>	Okpehe	High esterase activity (degradation of tributyrin) displayed by strains	Azokpota et al. 2006
	<i>B. subtilis</i>	Okpehe	Production of bacteriocin, which was identified as subtilisin, using subtilisin-specific primers and PCR amplification of the subtilisin gene. Bacteriocin was stable at 100 °C for 10 min and exhibited highest activity at pH values lower or equal to pH 6.0.	Oguntoyinbo et al. 2007
	<i>B. subtilis</i>	Soumbala and bikalga	Production of surfactins (C14 and C15).	Savadogo et al. 2011
	<i>B. subtilis</i> subsp. <i>subtilis</i>	Bikalga	Production of surfactin and a putative novel bacteriocin having a molecular weight of 3346.59 Da which is different from previously reported molecular weights of subtilin (3319.56 Da) and subtilisin (3400.57 Da) although the producing strain <i>B. subtilis</i> subsp. <i>subtilis</i> H4 possessed the genes involved in subtilin, subtilisin, surfactin and plipastatin biosynthesis. Inhibition of growth of <i>Listeria monocytogenes</i> , <i>Micrococcus luteus</i> , <i>Staph. aureus</i> and <i>B. cereus</i> .	Compaoré et al. 2013
	<i>B. subtilis</i>	Bikalga	Inhibited <i>B. cereus</i> , <i>Staphylococcus aureus</i> , <i>Escherichia coli</i> and caused abnormal germination of <i>Aspergillus ochraceus</i>	Ouoba et al. 2007
	<i>B. subtilis</i>	Maari	Production of bacteriocins; subtilisin and subtilin. Exhibits antimicrobial activity toward Gram positive and negative pathogens.	Kaboré et al. 2012
	<i>B. subtilis</i>	Maari	Bacteriocins production. Substrate-specific and strain-specific antimicrobial activity against <i>B. cereus</i>	Kaboré et al. 2013
	<i>B. amyloliquefaciens</i> subsp. <i>plantarum</i>	Bikalga	Exhibits broad spectrum antifungal and antibacterial properties through production of several lipopeptide antibiotics and dipeptide bacilysin	Compaoré et al. 2013

amino acids and ammonia from proteins (Table 2). Indeed, several studies have reported increasing protease activity from the onset of fermentation, leading to increase in the quantity of total free amino acids (FAA) and essential FAA, such as lysine, cysteine, methionine, leucine, isoleucine, tyrosine and phenylalanine (Omafuvbe, Shonukan, and Abiose 2000; Ouoba, Rechinger, et al. 2003; Pant et al. 2015; Parkouda et al. 2015; Terlabie, Sakyi-Dawson, and Amoa-Awua 2006). The profile of soluble proteins during seed fermentation have been shown to change with fermentation time and varies depending on fermenting strains (Ouoba, Rechinger, et al. 2003).

Degradation of non-digestible carbohydrates

Raw materials used to produce alkaline fermented condiments are rich in carbohydrates, of which a large proportion is non-digestible oligosaccharides (Akaaimo and Raji 2006; Ogbonna, Sokari, and Achinewhu 2001; Omafuvbe, Shonukan, and Abiose 2000; Sarkar et al. 1997). Stachyose, raffinose, sucrose and arabinogalactan constitute among others, the main poly- and oligosaccharides in legume seeds (Aderibigbe and Odunfa 1990; Karr-Lilienthal et al. 2005; Kiers, Rombouts, and Nout 2000; Odunfa 1983; Terlabie, Sakyi-Dawson, and Amoa-Awua 2006), which are the raw materials for the fermentation of West African condiments.

Some of these carbohydrates have been shown to be associated with abdominal distension and flatulence in humans (Naczka, Amarowicz, and Shahidi 1997; Sarkar et al. 1997). Microorganisms involved in the fermentation of protein-rich seeds into condiments hydrolyze the non-digestible carbohydrates, such as galactamannan, arabinogalactan, stachyose and raffinose into simple carbohydrates (melibiose, fructose and galactose), which are readily digestible by humans, and in addition positively influence the texture of the product by softening the plant tissue (Odunfa 1983; Ouoba, Diawara, Christensen, et al. 2007; Sarkar et al. 1997). Thus, *Bacillus* spp. are capable of producing amylase, galactanase, galactosidase, glucosidase and fructofuranosidase, which are enzymes involved in the degradation of complex carbohydrates during alkaline fermentation (Aderibigbe and Odunfa 1990; Dakwa et al. 2005; Kiers, Rombouts, and Nout 2000; Omafuvbe, Shonukan, and Abiose 2000; Parkouda, Diawara, and Debrah 2014; Sarkar et al. 1997; Terlabie, Sakyi-Dawson, and Amoa-Awua 2006).

Degradation of lipids

Similar to degradation of carbohydrates, several investigations on biochemical changes associated with alkaline fermentation of protein-rich legume seeds in West Africa reported changes in crude fat content and fatty acid profiles (Gernah, Inyang, and Ezeora 2007; Ogunshe, Omotosho, and Ayansina 2007; Omafuvbe, Shonukan, and Abiose 2000; Parkouda et al. 2015; Terlabie, Sakyi-Dawson, and Amoa-Awua 2006). Generally, increases in free fatty acids during alkaline fermentation have been reported (Ogunshe, Omotosho, and Ayansina 2007; Parkouda et al. 2015; Sarkar and Tamang 1995). However, for some products such as *dawadawa*, contradicting results have been reported. While Odunfa and Adesomoju (1985) reported a decrease in fatty acid concentration, Antai and Ibrahim (1986) reported an increase in the fatty acid concentration during *dawadawa* fermentation. *Bacillus* spp. involved in the alkaline fermentation of legume seeds have been shown to possess lipolytic activity (Table 2), a property that has been reported to be strain dependant (Ouoba, Cantor, et al. 2003).

Production of antimicrobial peptides by *Bacillus* in West African fermented condiments

The ability of fermentative microorganisms to produce antimicrobial peptides (AMPs) is a property that gives them superior ability to survive against other microorganisms in their immediate environment. In this way, the fermentative microorganisms possess the capability to naturally control pathogenic and spoilage microorganisms in the food environment, and likely also in the gut of consumers. Consequently, antimicrobial property is a relevant technological characteristic that is required for the selection of functional starter cultures, for the production of fermented food condiments with consistent quality and enhanced safety (Ouoba, Cantor, et al. 2003). In the case of *Bacillus* strains, the production of antimicrobial substances and sporulation

capacity give them a dual advantage, in terms of their ability to survive in different extreme environments, including food processing conditions.

Members of the genus *Bacillus* are known to produce a wide variety of peptides (Ongena and Jacques 2008) and non-peptide (Hamdache et al. 2011; Wise et al. 2012) antimicrobial compounds that contribute to the quality and safety attributes of fermented food condiments in West Africa. For example, *B. subtilis* group species isolated from West African fermented condiments are known to produce antimicrobial compounds that are effective against a number of foodborne pathogenic bacteria and fungi (Compaoré, Nielsen, Sawadogo-Lingani, et al. 2013; Compaoré, Nielsen, Ouoba, et al. 2013; Ouoba, Diawara, Jespersen, et al. 2007; Savadogo et al. 2011). The most important of these antimicrobial compounds are perhaps bacteriocins and the peptides group including lipopeptides (iturins, fengycins and surfactins).

Bacteriocin production

Bacteriocins are bacterial antimicrobial peptides or proteins produced by ribosomal synthesis to inhibit or kill other related or unrelated microorganisms (Abriouel et al. 2011; Cotter, Hill, and Ross 2005; Leroy and De Vuyst 2004). These metabolites are heterogeneous compounds that may have a narrow spectrum by inhibiting bacteria taxonomically close or a broad spectrum by inhibiting a wide variety of bacteria (Cotter, Hill, and Ross 2005; Leroy and De Vuyst 2004; Mills et al. 2011). Yet, many other similar antimicrobial substances that are not well characterized and the peptide nature of the antimicrobial compound not confirmed are often termed as bacteriocin-like inhibitory substances (BLIS). Generally, bacteriocins inhibit target cells by forming pores in the membrane, depleting the transmembrane potential and/or the pH gradient, resulting in the leakage of cellular materials (Cleveland et al. 2001). The proteinaceous nature of bacteriocins also implies a putative degradation in the gastrointestinal tract of humans and animals, making them suitable for use as natural preservatives in foods and feed (Cleveland et al. 2001).

B. subtilis, the predominant bacterial species in West African fermented condiments, is known to produce the bacteriocins. Bacteriocin producing strains of *B. subtilis* that exhibit antibacterial activity against foodborne pathogens, including *L. monocytogenes* and *B. cereus* were isolated from *maari* in Burkina Faso (Kaboré et al. 2013; Kaboré et al. 2012). The antimicrobial compound produced was confirmed to be proteinaceous in nature and heat stable, with activity over a wide range of pH (3–11). Further characterization revealed that the *B. subtilis* strains isolated from the West African fermented condiment, *maari*, harbored genes of the subtilisin operon (*sboA*), as well as, subtilin operon (*spaS*), but not *eriC* and *sunT* genes involved in ericin and sublancin synthesis, respectively (Kaboré et al. 2012). Furthermore, the genes involved in the biosynthesis of subtilin and subtilisin A were confirmed by sequencing of the related amplicons, which showed 96.2% similarity with the subtilin gene (*spaS*) from *B. subtilis* subsp. *spizizeni* strain

ATCC 6633 and 100% identity with the subtilisin A gene (*sboA*) from *B. subtilis* subsp. *subtilis* strain 168, respectively (Kaboré et al. 2012). Subtilin is a bacteriocin belonging to the class I bacteriocins or lantibiotics, and has been described as a nisin analogue. Class I lantibiotics are often referred to as autoinducing peptides (AIP) and are important in typical quorum sensing (QS) systems (Alvarez-Sieiro et al. 2016; Lubelski et al. 2008).

Lipopeptide antimicrobial production

Another important class of technologically relevant antimicrobial peptides commonly produced by *Bacillus* species are lipopeptides, which probably represent the most common class of secondary metabolites produced by *Bacillus* spp. (Stachelhaus, Mootz, and Marahiel 2002). *Bacillus* lipopeptides are synthesized by multienzyme complexes called Non-Ribosomal Peptide Synthetases (NRPS) (Marahiel and Essen 2009; Marahiel 1997), and exhibit a broad range of biological activities, with great potential for biotechnological applications in food, agricultural, medicine and the environment. In addition to their ability to inhibit the growth of several food-borne pathogens and/or spoilage microorganisms, their surfactant properties can positively affect the sensory characteristics, such as consistency and organoleptic attributes of food products.

Lipopeptide antimicrobials of *Bacillus* are classified into three different families, depending on the amino acid sequence, as surfactins/lichenysins, iturins (mycosubtilin, iturin A and bacillomycin), and fengycins/plipastatins (Ongena and Jacques 2008). *B. amyloliquefaciens* ssp. *plantarum* strains from *bikalga* exhibited both antibacterial and antifungal activities, and were revealed by PCR to harbor genes involved in the biosynthesis of the lipopeptides iturins (*ituA*, *ituD*, *ituC*), mycosubtilin (*myc*), bacillomycin (*bmyA*), surfactin (*srf*) and fengycin (*fen*); the polyketides macrolactin (*mlnA*), bacillaene (*baeA*) and difficidin (*dfnA*); and the dipeptide bacilysin (*bacA/B*) (Compaoré, Nielsen, Ouoba, et al. 2013). Furthermore, ultra-high-performance liquid chromatography-time of flight-mass spectrometry (U-HPLC-TOF-MS) analysis of antimicrobial substances produced by the *B. amyloliquefaciens* ssp. *plantarum* in BHI broth, enabled the identification of iturin, fengycin and surfactin. Similarly, *B. subtilis* subsp. *subtilis* H4 strain isolated from *bikalga* inhibited the growth of *L. monocytogenes*, *Micrococcus luteus*, *S. aureus* and *B. cereus*. A further characterization of the antimicrobial peptides showed that *B. subtilis* subsp. *subtilis* H4 harbored the genes involved in biosynthesis of subtilin (*spaS*, *etnS*), subtilisin (*yiwb*, *sboA*, *spoX*, *albA*), surfactin (*srfA*, *sfp*, *srflch*) and plipastatin (*pps*) (Compaoré, Nielsen, Ouoba, et al. 2013). Thus, *B. subtilis* subsp. *subtilis* H4 isolated from traditional *bikalga* in Burkina Faso co-produced surfactin and a novel bacteriocin with mass size of 3346.59 Da. (Compaoré, Nielsen, Ouoba, et al. 2013). In a related investigation, Savadogo et al. (2011) demonstrated that *B. subtilis* and *B. licheniformis* isolates from *soumbala* and *bikalga* produced surfactins, using both PCR and MALDI-TOF-MS analyses. In their study, two strains of *B. subtilis* produced biomolecules related to

surfactin C₁₄ and C₁₅, whereas *B. licheniformis* produced lichenysin, a lipopeptidic biosurfactant member of the family of surfactins (Savadogo et al. 2011). These surfactin molecules were further shown to be effectively synthesized by the *Bacillus* strains in *soumbala* by MALDI-TOF-MS analysis of crude extracts of *soumbala*, and the molecular structure of the surfactins was confirmed by LC-MS analysis (Savadogo et al. 2011). Kaboré et al. (2018) also reported that strains of *B. subtilis*, *B. pumilus* and *B. licheniformis* isolated from *maari* harbor *sfp* gene, responsible for the production of the lipopeptide biosurfactant, a member of the surfactin family. Furthermore, a relationship between the presence of the *sfp* gene in the *Bacillus* strains, biosurfactant production and antifungal activity against *Aspergillus flavus*, *A. niger*, *A. versicolor* and *Rhizopus oryzae* was demonstrated (Kaboré et al. 2018).

Microbiological safety of West African fermented seed condiments

In general, alkaline fermented condiments have been reported to be microbiologically safe (Steinkraus 1997) due to the production of antimicrobial peptides including bacteriocins and lipopeptide antimicrobials such as surfactins, iturins and fengycins by the predominant fermentation microorganisms. In addition to the antimicrobial effects exerted by these peptides, long cooking hours of seeds prior to fermentation during processing of West African seed condiments potentially eliminates non-spore forming pathogenic microorganisms (Parkouda et al. 2009). However, the spontaneous nature of the fermentation processes and poor control measures during and after processing predisposes these condiments to contamination by pathogenic microorganisms. Indeed, a number of secondary microorganisms including pathogenic bacteria and molds, and their toxins have been identified in West African fermented seed condiments. Specifically, pathogenic bacteria such as *B. cereus*, *Staphylococcus* spp., *E. coli*, *Salmonella* spp., *Shigella* spp., and *Clostridium* spp. as well as mycotoxigenic molds such as *A. flavus* and *A. parasiticus* have been isolated from West African alkaline fermented seed condiments, giving rise to food safety and public health concerns (Adekoya, Njobeh, et al. 2019; Adekoya, Obadina, et al. 2019; Parkouda et al. 2009).

The occurrence of *B. cereus* in West African alkaline fermented food condiments is prevalent and of considerable concern for food safety and health of the consuming public. *B. cereus* strains have been isolated in high numbers from several West African fermented seed condiments including *ogiri* and *okpehe* (Oguntinyinbo and Sanni 2007; Oguntinyinbo 2014; Okanlawon, Ogunbanwo, and Okunlola 2010), *ugba* (Ahaotu et al. 2013; Mbajunwa et al. 1998), *sonru*, *iru* and *afitin* (Azokpota, Hounhouigan, and Nago 2006; Azokpota et al. 2007; Thorsen et al. 2010), *ogiri* and *dawadawa* (Okanlawon, Ogunbanwo, and Okunlola 2010) and *bikalga* (Ouoba et al. 2008). *B. cereus* is recognized as an opportunistic human pathogen, capable of causing two types of food poisoning; emetic food poisoning resulting

from the production of heat stable toxin, cereulide, during growth in food, and diarrhoeal food poisoning, which results from the production of various enterotoxins in the small intestine of the host (Ehling-Schulz, Fricker, and Scherer 2004; Granum, Brynestad, and Kramer 1993). Diarrhoeal food poisoning has been linked to the enterotoxins cytotoxin (CytK), non-haemolytic enterotoxin (Nhe) and hemolysin BL (Hbl) (Agata et al. 1994; Michelet, Granum, and Mahillon 2005; Stenfors Arnesen, Fagerlund, and Granum 2008). Genes encoding production of non-haemolytic enterotoxin (NheA, NheB, NheC) and cytotoxin K (CytK) genes have been detected in *B. cereus* isolates from *ugba*, while Hbl genes (HblA, HblC, HblD) were detected in only one of six *B. cereus* isolates investigated from *ugba*. However, emetic-specific gene fragment was not detected in any of the *B. cereus* isolates from *ugba* (Ahaotu et al. 2013). Similarly, Ouoba et al. (2008) reported the presence of Nhe genes in all *B. cereus* isolates (100%) from *soumbala* and *bikalga*, while the CytK and Hbl genes were detected in 67% and 22% of *B. cereus* isolates respectively. Additionally, it was shown that *B. cereus* from *soumbala* and *bikalga* harboring NheA, NheB and NheC genes were able to produce the NheA component of the Nhe enterotoxin complex, in both laboratory broth and during the fermentation of African locust beans (Ouoba, Thorsen, and Varnam 2008). *B. cereus* isolates from *afitin*, *iru* and *sonru* have also been shown to harbor the enterotoxin genes *nhe* (A, B, C), the *hbl* (A, C, D), the CytK encoding gene, and *cesB*. Further, the *B. cereus* isolates from *afitin*, *iru* and *sonru* showed high levels of cytotoxicity in Vero cells assay comparable to diarrhoeal outbreak reference strains LWL3, LWL42, LWL90, B4AC and F4433/73NheA (Thorsen et al. 2010; Thorsen et al. 2011). In *okpehe*, 40% of the *B. cereus* strains were found to be toxigenic, and were capable of producing their toxins in mixed starter culture fermentation for *okpehe* production. Furthermore, PCR amplification of virulence genes revealed that *B. cereus* and *B. licheniformis* contained DNA sequences encoding the hemolysin BL (*hblD*) enterotoxin complex (Oguntoyinbo and Sanni 2007).

Another group of microorganisms that are commonly found in West African fermented seed condiments, with food safety and public health concern, are members of the genus *Staphylococcus*. In a recent study, Ouoba et al. (2019) reported the presence of coagulase negative (CoNS) and positive (CoPS) *Staphylococcus* species in alkaline fermented foods, using Rep-PCR/PFGE, and their associated toxins and antimicrobial resistance genetic elements. Specifically, the authors reported the presence of five species from *soumbala* (*S. epidermidis*, *S. pasteurii*, *S. condimenti*, *S. piscifermentans* and *S. simulans*) and four from *bikalga* (*S. aureus*, *S. cohnii*, *S. haemolyticus* and *M. caseolyticus*). While *nhe* toxin genes were not detected and the bacteria did not produce the staphylococcal enterotoxins A, B, C and D, antimicrobial resistance (AMR) genes including *blazA*, *cat501*, *dfr* (A), *dfr* (G), *mecA*, *mecA1*, *msr* (A) and *tet* (K) were identified in both CoNS and CoPS *Staphylococcus* species (Ouoba et al. 2019). The heterogeneity of *Staphylococcus* species from *bikalga* and *soumbala*, their relationship with clinical and

environmental isolates, as well as their safety, in relation to AMR and toxin production, underscores the importance of staphylococci in these products, particularly in relation to the safety of the consumers. From *iru* and *ogiri* condiments in Nigeria, other potentially pathogenic bacterial species such as *Alcaligenes faecalis*, *B. anthracis*, *Proteus mirabilis* and *S. sciuri* subsp. *sciuri* were detected although their toxin production profiles were not determined (Adedeji et al. 2017). On the other hand, the presence of *Acinetobacter baumannii*, *Clostridium sartagofum*, *E. casseliflavus*, *Comamonas testosteronii* and *Aeromonas* species were reported in *ugba* in Nigeria (Okorie et al. 2017). Adekoya et al. (2019) also reported the presence of high numbers of members of the *Enterobacteriaceae* family in Nigerian *ogiri*, *ugba* and *iru*, with *Sphingomonas paucimobilis* and *E. coli* being the dominant Gram-negative bacterial species detected. Additionally, high levels of bacterial endotoxins (up to 5.5×10^4 EU/g) were reported in the Nigerian fermented condiments *ogiri*, *ugba* and *iru* (Adekoya, Obadina, et al. 2019).

Considering that the major raw materials for the production of West African fermented condiments are seeds of both cultivated and wild leguminous plants, the potential for contamination by toxigenic fungi in these fermented condiments is high and therefore a valid food safety concern is the presence of mycotoxins in these products. Toxigenic molds producing different mycotoxins have been isolated from *ogiri*, *ugba* and *iru* in Nigeria. Strains of *A. flavus* and *A. parasiticus* from the condiments were found to produce aflatoxin B1 (27–7406 µg/kg), whereas *A. niger* strains produced Ochratoxin A (28–1302 µg/kg). Other toxigenic strains such as *A. versicolor*, *A. amstelodami*, and *A. sydowii*, producers of sterigmatocystin were also identified in the Nigerian alkaline fermented seed condiment (Adekoya, Njobeh, et al. 2019).

All these preceding reports raise genuine concerns about the microbiological safety and variability in quality of traditional fermented seed condiments as a result of poor-quality raw materials, spontaneous or mixed-culture fermentation, poor control of processing conditions, such as temperature and pH, inadequate hygienic practices and post-processing handling. This poses major challenges for the development and consumer acceptance of West African fermented seed condiments. There is, therefore, the need to institute measures geared toward enhancing the quality and safety of traditional West African fermented condiments. One of such measures would be the development and use of starter cultures, based on indigenous microbial consortia for controlled fermentation processes, while striving to preserve the unique qualities of these products. In order to guarantee quality and safety of West African fermented condiments for broader consumer acceptance, application of starter cultures should be implemented along with good manufacturing practices (GMP), vis-a-vis personal and environmental hygiene, supply of quality raw materials and potable water, and post-processing handling including packaging and storage (Peter-Ikechukwu et al. 2016).

In order to ensure consumer safety, it is strongly recommended that the selection of *Bacillus* strains to be used as starter cultures for West African fermented seed condiments have the qualified presumption of safety (QPS) or generally recognized as safe (GRAS) status. The QPS concept which was developed in 2003 provides a harmonized generic safety pre-appraisal of microorganisms that are intentionally added at different stages of food and feed chain. Under the QPS protocols, unambiguously defined biological taxonomic units (TUs) are assessed for their body of knowledge, their safety and their end use. That is, for a *Bacillus* strain (and for that matter any other microorganisms) to be included in the QPS list, it must have been unambiguously identified with its taxonomic identity based on the internationally accepted classification of the List of Prokaryotic Names with Standing in Nomenclature (Euzéby and Parte 2018) and the modifications that appear in the *International Journal of Systematic and Evolutionary Microbiology* (Oren and Garrity 2015). Additionally, the body of knowledge about the microbial strain which includes its history of use (Constable et al. 2007; Pariza et al. 2015), its ecology in the natural environment, clinical aspects, industrial applications and special properties are required for QPS status. Properties related to colonization ability and routes for dispersal, knowledge about the strain's interaction with other microorganisms, especially with respect to antagonism and competitive ability, are also relevant. Furthermore, safety concerns relating to potential presence of virulence factors and antimicrobial resistance that may contribute to the pathogenicity of the microorganism to humans and animals, and to the possible production of biologically active substances, such as antimicrobials and toxins must have been assessed (Herman et al. 2019).

Conclusion and future perspectives

The production and consumption of fermented seed condiments constitute an important part of the West African food heritage, and their value in the diet, nutrition and health, and economy of the people cannot be overemphasized. *Bacillus* species (particularly, the *B. subtilis* group) dominate the alkaline fermentation of traditional West African seed condiments and display a number of technological properties that are relevant for the development of functional starter cultures. At the same time, a huge diversity of secondary microflora whose technological roles in the fermentation process are not yet fully understood, if any at all, are also associated with fermented seed condiments in West Africa. This heterogeneous nature of the microbiota of West African fermented seed condiments leads to the presence of microbial pathogens liable to synthesize toxic by-products, such as bacterial toxins and mycotoxins, with implications for food safety assurance and public health.

As the world population continues to grow, with its accompanying urbanization and changing dietary patterns, there will be an increasing need for food that is safe, nutritious, healthy and convenient, and that can be produced in an environmentally sustainable manner. Traditional seed

fermentation in West Africa hold great prospects for food security and income generation, for example, through the development and industrialization of the production processes and the improvement of the traditional seed fermentation technologies to meet changing consumer preferences. In this respect, developing functional starter cultures for controlled fermentation process is crucial. This will require a rigorous selection and characterization of desirable microbes responsible for transforming raw seeds into traditional West African condiments. Characterization should include both whole-genome sequencing and detailed physiological description to ensure that strains are suitable for their intended purpose. Undoubtedly, developments in genomics, metagenomic and metabolomics analysis will play critical roles, by providing insights into the genes, structure, and function of these fermentation microorganisms, as well as allow innovative safety assessment and monitoring of fermentation processes.

Disclosure statement

The authors declare no conflict of interest.

ORCID

James Owusu-Kwarteng  <http://orcid.org/0000-0002-2703-3393>

References

- Abriouel, H., C. M. Franz, N. Ben Omar, and A. Gálvez. 2011. Diversity and applications of *Bacillus bacteriocins*. *FEMS Microbiology Reviews* 35 (1):201–32. doi: [10.1111/j.1574-6976.2010.00244.x](https://doi.org/10.1111/j.1574-6976.2010.00244.x).
- Achi, O. K. 1992. Microorganisms associated with natural fermentation of *Prosopis africana* seeds for the production of okpiye. *Plant Foods for Human Nutrition (Dordrecht, Netherlands)* 42 (4):297–304. doi: [10.1007/BF02194090](https://doi.org/10.1007/BF02194090).
- Achi, O. K. 2005. Traditional fermented protein condiments in Nigeria. *African Journal of Biotechnology* 4 (13):1612–1.
- Achi, O. K., I. C. Anokwuru, and F. C. Ogbo. 2007. Microbiological and chemical changes during fermentation of crabs for ogiri-nisiko production. *American Journal of Food Technology* 2:301–6.
- Adams, M. R. 1990. Topical aspects of fermented foods. *Trends in Food Science & Technology* 1:140–4. doi: [10.1016/0924-2244\(90\)90111-B](https://doi.org/10.1016/0924-2244(90)90111-B).
- Adediji, B. S., O. T. Ezeokoli, C. N. Ezekiel, A. O. Obadina, Y. M. Somorin, M. Sulyok, R. A. Adeleke, B. Warth, C. C. Nwangburuka, A. M. Omemu, et al. 2017. Bacterial species and mycotoxin contamination associated with locust bean, melon and their fermented products in south-western Nigeria. *International Journal of Food Microbiology* 258:73–80. doi: [10.1016/j.ijfoodmicro.2017.07.014](https://doi.org/10.1016/j.ijfoodmicro.2017.07.014).
- Adekoya, I., P. Njobeh, A. Obadina, S. Landschoot, K. Audenaert, S. Okoth, M. De Boevre, and S. De Saeger. 2019. Investigation of the metabolic profile and toxigenic variability of fungal species occurring in fermented foods and beverage from Nigeria and South Africa using UPLC-MS/MS. *Toxins* 11 (2):85. doi: [10.3390/toxins11020085](https://doi.org/10.3390/toxins11020085).
- Adekoya, I., A. Obadina, M. Olorunfemi, O. Akande, S. Landschoot, S. De Saeger, and P. Njobeh. 2019. Occurrence of bacteria and endotoxins in fermented foods and beverages from Nigeria and South Africa. *International Journal of Food Microbiology* 305:108251. doi: [10.1016/j.ijfoodmicro.2019.108251](https://doi.org/10.1016/j.ijfoodmicro.2019.108251).
- Ademola, O. M., T. E. Adeyemi, O. T. Ezeokoli, K. I. Ayeni, A. O. Obadina, Y. M. Somorin, A. M. Omemu, R. A. Adeleke, C. C.

- Nwangburuka, F. Oluwafemi, et al. 2018. Phylogenetic analyses of bacteria associated with the processing of iru and ogiri condiments. *Letters in Applied Microbiology* 67 (4):354–62. doi: [10.1111/lam.13040](https://doi.org/10.1111/lam.13040).
- Aderibigbe, E. Y., and S. A. Odunfa. 1990. Growth and extracellular enzyme production by strains of *Bacillus* species isolated from fermenting African locust bean, iru. *Journal of Applied Bacteriology* 69 (5):662–71. doi: [10.1111/j.1365-2672.1990.tb01560.x](https://doi.org/10.1111/j.1365-2672.1990.tb01560.x).
- Adeyemi, G. A. 2016. Bacterial diversity studies and probiotic functions of *Bacillus* species in fermented locust bean seeds (*Parkia biglobosa* Jacq. Benth). PhD thesis, University of Lagos, Nigeria.
- Adeyemi, G., S. Grover, C. Isanbor, and F. A. Oguntuyinbo. 2019. Phylogenetics, Safety and In Vitro Functional Properties of *Bacillus* Species Isolated from Iru, a Nigerian Fermented Condiment. *Microbiology and Biotechnology Letters* 47 (4):498–508. doi:[10.4014/mbi.1903.03005](https://doi.org/10.4014/mbi.1903.03005).
- Adeyemi, G. A., F. A. Oguntuyinbo, S. Keisam, W. Romi, and K. Jeyaram. 2013. Combination of culture-independent and culture-dependent molecular methods for the determination of bacterial community of iru, a fermented *Parkia biglobosa* seeds. *Frontiers in Microbiology* 3: 436. doi: [10.3389/fmicb.2012.00436](https://doi.org/10.3389/fmicb.2012.00436).
- Adeyemi, G. A., F. A. Oguntuyinbo, W. Romi, T. A. Singh, and K. Jeyaram. 2014. Genome subtyping of autochthonous *Bacillus* species isolated from Iru, a fermented *Parkia biglobosa* seed. *Food Biotechnology* 28 (3):250–68. doi: [10.1080/08905436.2014.931866](https://doi.org/10.1080/08905436.2014.931866).
- Agata, N., M. Mori, M. Ohta, S. Suwan, I. Ohtani, and M. Isobe. 1994. A novel dodecadepsipeptide, cereulide, isolated from *Bacillus cereus* causes vacuole formation in HEP-2 cells. *FEMS Microbiology Letters* 121 (1):31–4. doi: [10.1111/j.1574-6968.1994.tb07071.x](https://doi.org/10.1111/j.1574-6968.1994.tb07071.x).
- Agbobatinkpo, B. P., G. M. Tossou, L. Adinsi, H. N. Akissoe, and D. J. Hounhouigan. 2019. Optimal fermentation parameters for processing high quality African locust bean condiments. *Journal of Food Science and Technology* 56 (10):4648–57. doi: [10.1007/s13197-019-03916-1](https://doi.org/10.1007/s13197-019-03916-1).
- Agbobatinkpo, P. B., P. Azokpota, N. Akissoe, P. Kayode, R. Da Gbadji, and D. J. Hounhouigan. 2011. Indigenous perception and characterization of Yanyanku and Ikpiru: Two functional additives for the fermentation of African locust bean. *Ecology of Food and Nutrition* 50 (2):101–14. doi: [10.1080/03670244.2011.552369](https://doi.org/10.1080/03670244.2011.552369).
- Agbobatinkpo, P. B., L. Thorsen, D. S. Nielsen, P. Azokpota, N. Akissoe, J. D. Hounhouigan, and M. Jakobsen. 2013. Biodiversity of aerobic endospore-forming bacterial species occurring in Yanyanku and Ikpiru, fermented seeds of *Hibiscus sabdariffa* used to produce food condiments in Benin. *International Journal of Food Microbiology* 163 (2-3):231–8. doi: [10.1016/j.ijfoodmicro.2013.02.008](https://doi.org/10.1016/j.ijfoodmicro.2013.02.008).
- Agbobatinkpo, P. B., S. D. Dabade, F. Laleye, N. Akissoe, P. Azokpota, and J. D. Hounhouigan. 2012. Softening effect of Ikpiru and Yanyanku, two traditional additives used for the fermentation of African Locust Bean (*Parkia biglobosa*) seeds in Benin. *International Journal of Biological and Chemical Sciences* 6 (3):1281–92. doi: [10.4314/ijbcs.v6i3.31](https://doi.org/10.4314/ijbcs.v6i3.31).
- Ahaotu, I., A. Anyogu, O. H. Njoku, N. N. Odu, J. P. Sutherland, and L. I. I. Ouoba. 2013. Molecular identification and safety of *Bacillus* species involved in the fermentation of African oil beans (*Pentaclethra macrophylla* Benth) for production of Ugba. *International Journal of Food Microbiology* 162 (1):95–104. doi: [10.1016/j.ijfoodmicro.2013.01.001](https://doi.org/10.1016/j.ijfoodmicro.2013.01.001).
- Akaaimo, D. I., and A. O. Raji. 2006. Some physical and engineering properties of *Prosopis africana* seed. *Biosystems Engineering* 95 (2): 197–205. doi: [10.1016/j.biosystemseng.2006.06.005](https://doi.org/10.1016/j.biosystemseng.2006.06.005).
- Akanni, G. B., H. L. De Kock, Y. Naudé, and E. M. Buys. 2018. Volatile compounds produced by *Bacillus* species alkaline fermentation of bambara groundnut (*Vigna subterranean* (L.) Verdc) into a dawadawa-type African food condiment using headspace solid-phase microextraction and GC×GC–TOFMS. *International Journal of Food Properties* 21 (1):930–42. doi: [10.1080/10942912.2018.1460757](https://doi.org/10.1080/10942912.2018.1460757).
- Alvarez-Sieiro, P., M. Montalbán-López, D. Mu, and O. P. Kuipers. 2016. Bacteriocins of lactic acid bacteria: Extending the family. *Applied Microbiology and Biotechnology* 100 (7):2939–51. doi: [10.1007/s00253-016-7343-9](https://doi.org/10.1007/s00253-016-7343-9).
- Amoa-Awua, W. K., B. Awusi, M. Owusu, V. Appiah, H. Ofori, L. Thorsen, and L. Jespersen. 2014. Reducing the atypical odour of dawadawa: Effect of modification of fermentation conditions and post-fermentation treatment on the development of the atypical odour of dawadawa. *Food Control* 42:335–42. doi: [10.1016/j.food-cont.2014.02.016](https://doi.org/10.1016/j.food-cont.2014.02.016).
- Amoa-Awua, W. K., N. N. Terlabie, and E. Sakyi-Dawson. 2006. Screening of 42 *Bacillus* isolates for ability to ferment soybeans into dawadawa. *International Journal of Food Microbiology* 106 (3):343–7. doi: [10.1016/j.ijfoodmicro.2005.08.016](https://doi.org/10.1016/j.ijfoodmicro.2005.08.016).
- Antai, S. P., and M. H. Ibrahim. 1986. Micro-organisms associated with African locust bean (*Parkia filicoidea* Welw) fermentation for 'dawadawa' production. *Journal of Applied Bacteriology* 61 (2):145–8. doi: [10.1111/j.1365-2672.1986.tb04268.x](https://doi.org/10.1111/j.1365-2672.1986.tb04268.x).
- Azokpota, P., D. J. Hounhouigan, and M. C. Nago. 2006. Microbiological and chemical changes during the fermentation of African locust bean (*Parkia biglobosa*) to produce afitin, iru and sonru, three traditional condiments produced in Benin. *International Journal of Food Microbiology* 107 (3):304–9. doi: [10.1016/j.ijfoodmicro.2005.10.026](https://doi.org/10.1016/j.ijfoodmicro.2005.10.026).
- Azokpota, P., P. L. Moller, J. D. Houghouigan, and M. Jakobson. 2007. Biodiversity of predominant *Bacillus* isolated from afitin, iru and sonru at different fermentation time. *International Journal of Biological and Chemical Sciences* 1 (3):211–22.
- Azokpota, P., D. J. Hounhouigan, M. C. Nago, and M. Jakobsen. 2006. Esterase and protease activities of *Bacillus* spp. from afitin, iru and sonru; three African locust bean (*Parkia biglobosa*) condiments from Benin. *African Journal of Biotechnology* 5 (3):265–72.
- Azokpota, P., J. D. Hounhouigan, N. T. Annan, M. C. Nago, and M. Jakobsen. 2008. Diversity of volatile compounds of afitin, iru and sonru, three fermented food condiments from Benin. *World Journal of Microbiology and Biotechnology* 24 (6):879–85. doi: [10.1007/s11274-007-9542-0](https://doi.org/10.1007/s11274-007-9542-0).
- Azokpota, P., J. D. Hounhouigan, N. T. Annan, T. Odjo, M. C. Nago, and M. Jakobsen. 2010. Volatile compounds profile and sensory evaluation of Beninese condiments produced by inocula of *Bacillus subtilis*. *Journal of the Science of Food and Agriculture* 90 (3):438–44. doi: [10.1002/jsfa.3835](https://doi.org/10.1002/jsfa.3835).
- Bassler, B. L. 2002. Small talk. Cell-to-cell communication in bacteria. *Cell* 109 (4):421–4. doi: [10.1016/s0092-8674\(02\)00749-3](https://doi.org/10.1016/s0092-8674(02)00749-3).
- Bassler, B. L., and R. Losick. 2006. Bacterially speaking. *Cell* 125 (2): 237–46. doi: [10.1016/j.cell.2006.04.001](https://doi.org/10.1016/j.cell.2006.04.001).
- Beaumont, M. 2002. Flavouring composition prepared by fermentation with *Bacillus* spp. *International Journal of Food Microbiology* 75 (3): 189–96. doi: [10.1016/S0168-1605\(01\)00706-1](https://doi.org/10.1016/S0168-1605(01)00706-1).
- Chadare, F. J., Jonkman, J. J. Wolkers-Rooijackers, Martinus, J. R. Nout, J. D. Hounhouigan, and M. H. Zwietering. 2011. Microbiota of Tayohounta, a fermented baobab flavour food of Benin. *African Journal of Biotechnology* 10 (69):15607–15.
- Chun, B. H., K. H. Kim, S. E. Jeong, and C. O. Jeon. 2020. The effect of salt concentrations on the fermentation of doenjang, a traditional Korean fermented soybean paste. *Food Microbiology* 86:103329. doi: [10.1016/j.fm.2019.103329](https://doi.org/10.1016/j.fm.2019.103329).
- Cleveland, J., T. J. Montville, I. F. Nes, and M. L. Chikindas. 2001. Bacteriocins: Safe, natural antimicrobials for food preservation. *International Journal of Food Microbiology* 71 (1):1–20. doi: [10.1016/S0168-1605\(01\)00560-8](https://doi.org/10.1016/S0168-1605(01)00560-8).
- Compaoré, C. S., D. S. Nielsen, L. I. I. Ouoba, T. S. Berner, K. F. Nielsen, H. Sawadogo-Lingani, B. Diawara, G. A. Ouédraogo, M. Jakobsen, and L. Thorsen. 2013. Co-production of surfactin and a novel bacteriocin by *Bacillus subtilis* subsp. *subtilis* H4 isolated from Bikalga, an African alkaline *Hibiscus sabdariffa* seed fermented condiment. *International Journal of Food Microbiology* 162 (3):297–307. doi: [10.1016/j.ijfoodmicro.2013.01.013](https://doi.org/10.1016/j.ijfoodmicro.2013.01.013).
- Compaoré, C. S., D. S. Nielsen, H. Sawadogo-Lingani, T. S. Berner, K. F. Nielsen, D. B. Adimpong, B. Diawara, G. A. Ouédraogo, M. Jakobsen, and L. Thorsen. 2013. *Bacillus amyloliquefaciens* ssp. *plantarum* strains as potential protective starter cultures for the production of Bikalga, an alkaline fermented

- food. *Journal of Applied Microbiology* 115 (1):133–46. doi: [10.1111/jam.12214](https://doi.org/10.1111/jam.12214).
- Constable, A., D. Jonas, A. Cockburn, A. Davi, G. Edwards, P. Hepburn, C. Herouet-Guicheney, M. Knowles, B. Moseley, R. Oberdörfer, et al. 2007. History of safe use as applied to the safety assessment of novel foods and foods derived from genetically modified organisms. *Food and Chemical Toxicology* 45 (12):2513–25. doi: [10.1016/j.fct.2007.05.028](https://doi.org/10.1016/j.fct.2007.05.028).
- Cotter, P. D., C. Hill, and R. P. Ross. 2005. Bacteriocins: Developing innate immunity for food. *Nature Reviews. Microbiology* 3 (10): 777–88. doi: [10.1038/nrmicro1273](https://doi.org/10.1038/nrmicro1273).
- Coughlan, L. M., P. D. Cotter, C. Hill, and A. Alvarez-Ordóñez. 2016. New weapons to fight old enemies: Novel strategies for the (Bio)control of Bacterial Biofilms in the Food Industry. *Frontiers in Microbiology* 7:1641 doi: [10.3389/fmicb.2016.01641](https://doi.org/10.3389/fmicb.2016.01641).
- Dakwa, S., E. Sakyi-Dawson, C. Diako, N. T. Annan, and W. Kofi Amoa-Awua. 2005. Effect of boiling and roasting on the fermentation of soybeans into dawadawa (soy-dawadawa). *International Journal of Food Microbiology* 104 (1):69–82. doi: [10.1016/j.ijfoodmicro.2005.02.006](https://doi.org/10.1016/j.ijfoodmicro.2005.02.006).
- Di Cagno, R., M. D. Angelis, R. Coda, F. Minervini, and M. Gobbetti. 2009. Molecular adaptation of sourdough *Lactobacillus plantarum* DC400 under co-cultivation with other lactobacilli. *Research in Microbiology* 160 (5):358–66. doi: [10.1016/j.resmic.2009.04.006](https://doi.org/10.1016/j.resmic.2009.04.006).
- Diaz, M., L. Kellingray, N. Akinyemi, O. O. Adefiranye, A. B. Olaonipekun, G. R. Bayili, J. Ibezim, A. S. Du Plessis, M. Houngbédji, D. Kamya, et al. 2019. Comparison of the microbial composition of African fermented foods using amplicon sequencing. *Scientific Reports* 9 (1):1–8. doi: [10.1038/s41598-019-50190-4](https://doi.org/10.1038/s41598-019-50190-4).
- Ehling-Schulz, M., M. Fricker, and S. Scherer. 2004. *Bacillus cereus*, the causative agent of an emetic type of food-borne illness. *Molecular Nutrition & Food Research* 48 (7):479–87.
- Euzéby, J. P., and J. P. Parte. 2018. List of prokaryotic names with standing in nomenclature. 2013.
- Ezeokoli, O., A. Gupta, T. Popoola, and C. Bezuidenhout. 2016. Molecular analysis of bacterial community dynamics during the fermentation of soy-daddawa condiment. *Food Science and Biotechnology* 25 (4):1081–6. doi: [10.1007/s10068-016-0174-8](https://doi.org/10.1007/s10068-016-0174-8).
- Ezeokoli, O. T., A. K. Gupta, C. Mienie, T. O. Popoola, and C. C. Bezuidenhout. 2016. PCR-denaturing gradient gel electrophoresis analysis of microbial community in soy-daddawa, a Nigerian fermented soybean (*Glycine max* (L.) Merr.) condiment. *International Journal of Food Microbiology* 220:58–62. doi: [10.1016/j.ijfoodmicro.2016.01.003](https://doi.org/10.1016/j.ijfoodmicro.2016.01.003).
- Gernah, D. I., C. U. Inyang, and N. L. Ezeora. 2007. Incubation and fermentation of African locust beans (*Parkia biglobosa*) in production of “Dawadawa.” *Journal of Food Processing and Preservation* 31 (2):227–39. doi: [10.1111/j.1745-4549.2007.00109.x](https://doi.org/10.1111/j.1745-4549.2007.00109.x).
- Gori, K., S. Moslehi-Jenabian, M. Purrotti, and L. Jespersen. 2011. Autoinducer-2 activity produced by bacteria found in smear of surface ripened cheeses. *International Dairy Journal* 21 (1):48–53. doi: [10.1016/j.idairyj.2010.06.009](https://doi.org/10.1016/j.idairyj.2010.06.009).
- Granum, P. E., S. Brynestad, and J. M. Kramer. 1993. Analysis of enterotoxin production by *Bacillus cereus* from dairy products, food poisoning incidents and non-gastrointestinal infections. *International Journal of Food Microbiology* 17 (4):269–79. doi: [10.1016/0168-1605\(93\)90197-o](https://doi.org/10.1016/0168-1605(93)90197-o).
- Hamdache, A., A. Lamarti, J. Aleu, and I. G. Collado. 2011. Non-peptide metabolites from the genus *Bacillus*. *Journal of Natural Products* 74 (4):893–9. doi: [10.1021/np100853e](https://doi.org/10.1021/np100853e).
- Henke, J. M., and B. L. Bassler. 2004. Quorum sensing regulates type III secretion in *Vibrio harveyi* and *Vibrio parahaemolyticus*. *Journal of Bacteriology* 186 (12):3794–805. doi: [10.1128/JB.186.12.3794-3805.2004](https://doi.org/10.1128/JB.186.12.3794-3805.2004).
- Herman, L., M. Chemaly, P. S. Cocconcelli, P. Fernandez, G. Klein, L. Peixe, M. Prieto, A. Querol, J. E. Suarez, I. Sundh, et al. 2019. The qualified presumption of safety assessment and its role in EFSA risk evaluations: 15 years past. *FEMS Microbiology Letters* 366 (1): i17–i23. doi: [10.1093/femsle/fny260s](https://doi.org/10.1093/femsle/fny260s).
- Humblot, C., and J.-P. Guyot. 2009. Pyrosequencing of tagged 16S rRNA gene amplicons for rapid deciphering of the microbiomes of fermented foods such as pearl millet slurries. *Applied and Environmental Microbiology* 75 (13):4354–61. doi: [10.1128/AEM.00451-09](https://doi.org/10.1128/AEM.00451-09).
- Isu, N. R., and H. O. Njoku. 1997. An evaluation of the microflora associated with fermented African oil bean (*Pentaclethra macrophylla* Benth) seeds during ugba production. *Plant Foods for Human Nutrition* 51 (2):145–57.
- Jeff-Agboola, Y. A. 2007. Microorganisms associated with natural fermentation of African yam bean (*Sphenostylis sternocarpa* Harms) seeds for the production of otiru. *Research Journal of Microbiology* 2 (11):816–23. doi: [10.3923/jm.2007.816.823](https://doi.org/10.3923/jm.2007.816.823).
- Jeyaram, K., W. Romi, T. A. Singh, G. A. Adewumi, K. Basanti, and F. A. Oguntuyinbo. 2011. Distinct differentiation of closely related species of *Bacillus subtilis* group with industrial importance. *Journal of Microbiological Methods* 87 (2):161–4. doi: [10.1016/j.mimet.2011.08.011](https://doi.org/10.1016/j.mimet.2011.08.011).
- Jung, J. Y., S. H. Lee, J. M. Kim, M. S. Park, J.-W. Bae, Y. Hahn, E. L. Madsen, and C. O. Jeon. 2011. Metagenomic analysis of kimchi, a traditional Korean fermented food. *Applied and Environmental Microbiology* 77 (7):2264–74. doi: [10.1128/AEM.02157-10](https://doi.org/10.1128/AEM.02157-10).
- Jung, W. Y., J. Y. Jung, H. Jung Lee, and C. O. Jeon. 2016. Functional characterization of bacterial communities responsible for fermentation of Doenjang: A traditional Korean fermented soybean paste. *Frontiers in Microbiology* 7:827 doi: [10.3389/fmicb.2016.00827](https://doi.org/10.3389/fmicb.2016.00827).
- Kaboré, D., M. Gagnon, D. Roy, H. Sawadogo-Lingani, B. Diawara, and G. LaPointe. 2018. Rapid screening of starter cultures for maari based on antifungal properties. *Microbiological Research* 207:66–74. doi: [10.1016/j.micres.2017.11.005](https://doi.org/10.1016/j.micres.2017.11.005).
- Kaboré, D., D. Sandris Nielsen, H. Sawadogo-Lingani, B. Diawara, M. H. Dicko, M. Jakobsen, and L. Thorsen. 2013. Inhibition of *Bacillus cereus* growth by bacteriocin producing *Bacillus subtilis* isolated from fermented baobab seeds (maari) is substrate dependent. *International Journal of Food Microbiology* 162 (1):114–9. doi: [10.1016/j.ijfoodmicro.2012.12.027](https://doi.org/10.1016/j.ijfoodmicro.2012.12.027).
- Kaboré, D., L. Thorsen, D. Sandris Nielsen, T. S. Berner, H. Sawadogo-Lingani, B. Diawara, M. H. Dicko, and M. Jakobsen. 2012. Bacteriocin formation by dominant aerobic sporeformers isolated from traditional maari. *International Journal of Food Microbiology* 154 (1-2):10–8. doi: [10.1016/j.ijfoodmicro.2011.12.003](https://doi.org/10.1016/j.ijfoodmicro.2011.12.003).
- Karr-Lilienthal, L. K., C. T. Kadzere, C. M. Grieshop, and G. C. Fahey, Jr. 2005. Chemical and nutritional properties of soybean carbohydrates as related to nonruminants: A review. *Livestock Production Science* 97 (1):1–12. doi: [10.1016/j.livprodsci.2005.01.015](https://doi.org/10.1016/j.livprodsci.2005.01.015).
- Kiers, J. L., A. E. Van Laeken, F. M. Rombouts, and M. J. Nout. 2000. In vitro digestibility of *Bacillus* fermented soya bean. *International Journal of Food Microbiology* 60 (2-3):163–9. doi: [10.1016/S0168-1605\(00\)00308-1](https://doi.org/10.1016/S0168-1605(00)00308-1).
- Kim, Y.-S., M.-C. Kim, S.-W. Kwon, S.-J. Kim, I.-C. Park, J.-O. Ka, and H.-Y. Weon. 2011. Analyses of bacterial communities in meju, a Korean traditional fermented soybean bricks, by cultivation-based and pyrosequencing methods. *Journal of Microbiology (Seoul, Korea)* 49 (3):340–8. doi: [10.1007/s12275-011-0302-3](https://doi.org/10.1007/s12275-011-0302-3).
- Kpikpi, E., Nayra, R. L. Glover, V. P. Dzogbefia, D. S. Nielsen, and M. Jakobsen. 2010. Isolation of lactic acid bacteria from kantong, a condiment produced from the fermentation of kapok (*Ceiba pentandra*) seeds and cassava (*Manihot esculentum*) flour. *Report and Opinion* 2 (8):1–7.
- Kwak, C. S., M. S. Lee, S. I. Oh, 2010. Discovery of novel sources of vitamin B12 in traditional Korean foods from nutritional surveys of centenarians. *Current Gerontology and Geriatrics Research* 2010: 1–11. and, S. C. Park. 2010. doi: [10.1155/2010/374897](https://doi.org/10.1155/2010/374897).
- Leejeerajumnean, A., S. C. Duckham, J. D. Owens, and J. M. Ames. 2001. Volatile compounds in *Bacillus*-fermented soybeans. *Journal of the Science of Food and Agriculture* 81 (5):525–9. doi: [10.1002/jsfa.843](https://doi.org/10.1002/jsfa.843).
- Leroy, F., and L. De Vuyst. 2004. Lactic acid bacteria as functional starter cultures for the food fermentation industry. *Trends in Food Science & Technology* 15 (2):67–78. doi: [10.1016/j.tifs.2003.09.004](https://doi.org/10.1016/j.tifs.2003.09.004).

- Lubelski, J., R. Rink, R. Khusainov, G. N. Moll, and O. P. Kuipers. 2008. Biosynthesis, immunity, regulation, mode of action and engineering of the model lantibiotic nisin. *Cellular and Molecular Life Sciences : CMLS* 65 (3):455–76. doi: [10.1007/s00018-007-7171-2](https://doi.org/10.1007/s00018-007-7171-2).
- Makanjuola, O. M., and A. Ajayi. 2012. Effect of natural fermentation on the nutritive value and mineral composition of African locust beans. *Pakistan Journal of Nutrition* 11 (1):11–3. doi: [10.3923/pjn.2012.11.13](https://doi.org/10.3923/pjn.2012.11.13).
- Marahiel, M. A., and L. -O. Essen. 2009. Chapter 13. Nonribosomal peptide synthetases mechanistic and structural aspects of essential domains. *Methods in Enzymology* 458:337–51. doi: [10.1016/S0076-6879\(09\)04813-7](https://doi.org/10.1016/S0076-6879(09)04813-7).
- Marahiel, M. A. 1997. Protein templates for the biosynthesis of peptide antibiotics. *Chemistry & Biology* 4 (8):561–7. doi: [10.1016/S1074-5521\(97\)90242-8](https://doi.org/10.1016/S1074-5521(97)90242-8).
- Mbajunwa, O. K., J. O. Akingbala, K. Mulongoy, and G. Oguntimein. 1998. Starter culture evaluation for the production of ugba from African oil bean seed *Pentaclethra macrophylla*. *Journal of the Science of Food and Agriculture* 77 (1):127–32. doi: [10.1002/\(SICI\)1097-0010\(199805\)77:1<127::AID-JSFA17>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1097-0010(199805)77:1<127::AID-JSFA17>3.0.CO;2-4).
- Meerak, J., P. Yukphan, M. Miyashita, H. Sato, Y. Nakagawa, and Y. Tahara. 2008. Phylogeny of gamma-polyglutamic acid-producing *Bacillus* strains isolated from a fermented locust bean product manufactured in West Africa. *The Journal of General and Applied Microbiology* 54 (3):159–66. doi: [10.2323/jgam.54.159](https://doi.org/10.2323/jgam.54.159).
- Michelet, N., P. E. Granum, and J. Mahillon. 2005. *Bacillus cereus* enterotoxins, bi- and tri-component cytolytins and other haemolysins.
- Mills, S., C. Stanton, C. Hill, and R. P. Ross. 2011. New developments and applications of bacteriocins and peptides in foods. *Annual Review of Food Science and Technology* 2:299–329. doi: [10.1146/annurev-food-022510-133721](https://doi.org/10.1146/annurev-food-022510-133721).
- Mohamadou, B.-A., C. M., Mbofung, and G. Barbier. 2013. Genotypic and phenotypic diversity among *Bacillus* species isolated from Mbuja, a Cameroonian traditional fermented condiment. *African Journal of Biotechnology* 12 (12): 1335–43.
- Moslehi-Jenabian, S., K. Gori, and L. Jespersen. 2009. AI-2 signalling is induced by acidic shock in probiotic strains of *Lactobacillus* spp. *International Journal of Food Microbiology* 135 (3):295–302. doi: [10.1016/j.ijfoodmicro.2009.08.011](https://doi.org/10.1016/j.ijfoodmicro.2009.08.011).
- N'dir, B., Rokhaya, D. Gningue, Ng Keita, M. Souane, L. Laurent, C. Cornelius, and P. Thonart. 1997. Microbiological and organoleptic characteristics of commercial netetu. *Cahiers d'Etudes et de Recherches Francophones Agricoles (France)*.
- N'Dir, Babacar, C., Hbid, C. Cornélius, D. Roblain, P. Jacques, F. Vanhentenryck, M. Diop, and P. Thonart. 1994. Propriétés antifongiques de la microflore sporulée du "nétetu. *Cahiers Agricoles* 3 (1):23–30. 1).
- Naczek, M., R. Amarowicz, and F. Shahidi. 1997. α -Galactosides of sucrose in foods: composition, flatulence-causing effects, and removal. ACS Publications.
- Nam, Y.-D., S.-H. Yi, and S.-I. Lim. 2012. Bacterial diversity of cheonggukjang, a traditional Korean fermented food, analyzed by barcoded pyrosequencing. *Food Control* 28 (1):135–42. doi: [10.1016/j.foodcont.2012.04.028](https://doi.org/10.1016/j.foodcont.2012.04.028).
- Obadina, A. O., O. B. Oyewole, L. O. Sanni, K. I. Tomlins, and A. Westby. 2008. Identification of hazards and critical control points (CCP) for cassava fufu processing in South-West Nigeria. *Food Control* 19 (1):22–6. doi: [10.1016/j.foodcont.2007.01.002](https://doi.org/10.1016/j.foodcont.2007.01.002).
- Obeta, J. A. N. 1983. A note on the micro-organisms associated with the fermentation of seeds of the African oil bean tree (*Pentaclethra macrophylla*). *Journal of Applied Bacteriology* 54 (3):433–5. doi: [10.1111/j.1365-2672.1983.tb02639.x](https://doi.org/10.1111/j.1365-2672.1983.tb02639.x).
- Odufa, S. A. 1981. Microorganisms associated with fermentation of African locust bean (*Parkia filicoidea*) during iru preparation. *Journal of Plant Foods* 3 (4):245–50. doi: [10.1080/0142968X.1981.11904236](https://doi.org/10.1080/0142968X.1981.11904236).
- Odufa, S. A. 1983. Carbohydrate changes in fermenting locust bean (*Parkia filicoidea*) during iru preparation. *Qualitas Plantarum Plant Foods for Human Nutrition* 32 (1):3–10. doi: [10.1007/BF01093924](https://doi.org/10.1007/BF01093924).
- Odufa, S. A. 1985. Biochemical changes in fermenting African locust bean (*Parkia biglobosa*) during 'iru' fermentation. *International Journal of Food Science & Technology* 20 (3):295–303. doi: [10.1111/j.1365-2621.1985.tb00379.x](https://doi.org/10.1111/j.1365-2621.1985.tb00379.x).
- Odufa, S. A., and A. Adesomoju. 1986. Fatty acid composition of African locust bean (*Parkia biglobosa*). *Chemie, Mikrobiologie, Technologie Der Lebensmittel* 10 (3-4):125–7.
- Odufa, S. A., and A. A. Adesomoju. 1985. Effects of fermentation on the free fatty acids of African locust bean during iru production. *Journal of Plant Foods* 6 (2):111–5. doi: [10.1080/0142968X.1985.11904303](https://doi.org/10.1080/0142968X.1985.11904303).
- Ogbadu, L., and R. N. Okagbue. 1988. Bacterial fermentation of soya bean for 'daddawa' production. *Journal of Applied Bacteriology* 65 (5): 353–6. doi: [10.1111/j.1365-2672.1988.tb01902.x](https://doi.org/10.1111/j.1365-2672.1988.tb01902.x).
- Ogbonna, D. N., T. G. Sokari, and S. C. Achinewhu. 2001. Development of an owoh-type product from African yam beans (*Sphenostylis stenocarpa*) (Hoechst (ex. A. Rich.) Harms.) seeds by solid substrate fermentation. *Plant Foods for Human Nutrition (Dordrecht, Netherlands)* 56 (2):183–94. doi: [10.1023/a:1011185513717](https://doi.org/10.1023/a:1011185513717).
- Ogunshe, A. A., M. O. Omotosho, and A. D. V. Ayansina. 2007. Microbial studies and biochemical characteristics of controlled fermented afiyo-a Nigerian fermented food condiment from *Prosopis africana* (Guill and Perr.) Taub. *Pakistan Journal of Nutrition* 6 (6): 620–7. doi: [10.3923/pjn.2007.620.627](https://doi.org/10.3923/pjn.2007.620.627).
- Oguntuyinbo, F. A., and A. I. Sanni. 2007. Determination of toxigenic potentials of *Bacillus* strains isolated from Okpehe, a Nigerian fermented condiment. *World Journal of Microbiology and Biotechnology* 23 (1):65–70. doi: [10.1007/s11274-006-9193-6](https://doi.org/10.1007/s11274-006-9193-6).
- Oguntuyinbo, F. A., M. Huch, G.-S. Cho, U. Schillinger, W. H. Holzapfel, A. I. Sanni, and C. M. Franz. 2010. Diversity of *Bacillus* species isolated from okpehe, a traditional fermented soup condiment from Nigeria. *Journal of Food Protection* 73 (5):870–8. doi: [10.4315/0362-028x-73.5.870](https://doi.org/10.4315/0362-028x-73.5.870).
- Oguntuyinbo, F. A., A. I. Sanni, C. M. Franz, and W. H. Holzapfel. 2007. In vitro fermentation studies for selection and evaluation of *Bacillus* strains as starter cultures for the production of okpehe, a traditional African fermented condiment. *International Journal of Food Microbiology* 113 (2):208–18. doi: [10.1016/j.ijfoodmicro.2006.07.006](https://doi.org/10.1016/j.ijfoodmicro.2006.07.006).
- Oguntuyinbo, F. A. 2014. Safety challenges associated with traditional foods of West Africa. *Food Reviews International* 30 (4):338–58. doi: [10.1080/87559129.2014.940086](https://doi.org/10.1080/87559129.2014.940086).
- Okanlawon, B. M., St Ogunbanwo, and A. O. Okunlola. 2010. Growth of *Bacillus cereus* isolated from some traditional condiments under different regimens. *African Journal of Biotechnology* 9 (14):2129–35.
- Okechukwu, R. I., N. Ewelike, and A. A. Ukaoma. 2012. Changes in the nutrient composition of the African oil bean meal "ugba" (*Pentaclethra macrophylla* Benth) subjected to solid state natural fermentation. *Journal of Applied Bioscience* 51:3591–95.
- Okorie, C. P., and N. A. Olasupo. 2013a. Controlled fermentation and preservation of UGBA -an indigenous Nigerian fermented food. *SpringerPlus* 2 (1):470. doi: [10.1186/2193-1801-2-470](https://doi.org/10.1186/2193-1801-2-470).
- Okorie, P. C., and N. A. Olasupo. 2013b. Growth and extracellular enzyme production by microorganisms isolated from Ugba-an indigenous Nigerian fermented condiment. *African Journal of Biotechnology* 12 (26): 4158–67.
- Okorie, P. C., N. A. Olasupo, F. N. Anike, G. N. Elemo, and O. S. Isikhuemhen. 2017. Incidence of enteric pathogens in ugba, a traditional fermented food from African oil bean seeds (*Pentaclethra macrophylla*). *International Journal of Food Contamination* 4 (1):12. doi: [10.1186/s40550-017-0057-7](https://doi.org/10.1186/s40550-017-0057-7).
- Omafuvbe, B. O., O. O. Shonukan, and S. H. Abiose. 2000. Microbiological and biochemical changes in the traditional fermentation of soybean for 'soy-daddawa'—Nigerian food condiment. *Food Microbiology* 17 (5):469–74. doi: [10.1006/fmic.1999.0332](https://doi.org/10.1006/fmic.1999.0332).
- Omafuvbe, B. O., O. S. Falade, B. A. Osuntogun, and S. R. Adewusi. 2004. Chemical and biochemical changes in African locust bean (*Parkia biglobosa*) and melon (*Citrullus vulgaris*) seeds during fermentation to condiments. *Pak. J. Nutr* 3 (3):140–5.

- Ongena, M., and P. Jacques. 2008. Bacillus lipopeptides: Versatile weapons for plant disease biocontrol. *Trends in Microbiology* 16 (3): 115–25. doi: [10.1016/j.tim.2007.12.009](https://doi.org/10.1016/j.tim.2007.12.009).
- Oren, A., and G. M. Garrity. 2015. List of new names and new combinations previously effectively, but not validly published. Validation list no. 165. *International Journal of Systematic and Evolutionary Microbiology* 65 (Pt_9):2777–83. doi: [10.1099/ijsem.0.000464](https://doi.org/10.1099/ijsem.0.000464).
- Ouoba, L. I. I., A. B. V. Mbozo, A. Anyogu, P. I. Obioha, H. Lingani-Sawadogo, J. P. Sutherland, L. Jespersen, and H. B. Ghoddusi. 2019. Environmental heterogeneity of Staphylococcus species from alkaline fermented foods and associated toxins and antimicrobial resistance genetic elements. *International Journal of Food Microbiology* 311: 108356 doi: [10.1016/j.jfoodmicro.2019.108356](https://doi.org/10.1016/j.jfoodmicro.2019.108356).
- Ouoba, L. I. I., L. Thorsen, and A. H. Varnam. 2008. Enterotoxins and emetic toxins production by Bacillus cereus and other species of Bacillus isolated from Soumbala and Bikalga, African alkaline fermented food condiments. *International Journal of Food Microbiology* 124 (3):224–30. doi: [10.1016/j.jfoodmicro.2008.03.026](https://doi.org/10.1016/j.jfoodmicro.2008.03.026).
- Ouoba, L. I., Ivette, B. Diawara, L. Jespersen, and M. Jakobsen. 2007. Antimicrobial activity of Bacillus subtilis and Bacillus pumilus during the fermentation of African locust bean (Parkia biglobosa) for Soumbala production. *Journal of Applied Microbiology* 102 (4):963–70.
- Ouoba, L. I. I., B. Diawara, T. Christensen, J. D. Mikkelsen, and M. Jakobsen. 2007. Degradation of polysaccharides and non-digestible oligosaccharides by Bacillus subtilis and Bacillus pumilus isolated from Soumbala, a fermented African locust bean (Parkia biglobosa) food Condiment. *European Food Research and Technology* 224 (6): 689–94. doi: [10.1007/s00217-006-0359-0](https://doi.org/10.1007/s00217-006-0359-0).
- Ouoba, L. I. I., B. Diawara, W. k Amoa-Awua, A. S. Traoré, and P. L. Møller. 2004. Genotyping of starter cultures of Bacillus subtilis and Bacillus pumilus for fermentation of African locust bean (Parkia biglobosa) to produce Soumbala. *International Journal of Food Microbiology* 90 (2):197–205. doi: [10.1016/s0168-1605\(03\)00302-7](https://doi.org/10.1016/s0168-1605(03)00302-7).
- Ouoba, L. I. I., M. D. Cantor, B. Diawara, A. S. Traore, and M. Jakobsen. 2003. Degradation of African locust bean oil by Bacillus subtilis and Bacillus pumilus isolated from soumbala, a fermented African locust bean condiment. *Journal of Applied Microbiology* 95 (4):868–73. doi: [10.1046/j.1365-2672.2003.02063.x](https://doi.org/10.1046/j.1365-2672.2003.02063.x).
- Ouoba, L. I. I., B. Diawara, N. T. Annan, L. Poll, and M. Jakobsen. 2005. Volatile compounds of Soumbala, a fermented African locust bean (Parkia biglobosa) food condiment. *Journal of Applied Microbiology* 99 (6):1413–21. doi: [10.1111/j.1365-2672.2005.02722.x](https://doi.org/10.1111/j.1365-2672.2005.02722.x).
- Ouoba, L. I. I., C. A. G. Nyanga-Koumou, C. Parkouda, H. Sawadogo, S. C. Kobawila, S. Keleke, B. Diawara, D. Louembe, and J. P. Sutherland. 2010. Genotypic diversity of lactic acid bacteria isolated from African traditional alkaline-fermented foods. *Journal of Applied Microbiology* 108 (6):2019–29. doi: [10.1111/j.1365-2672.2009.04603.x](https://doi.org/10.1111/j.1365-2672.2009.04603.x).
- Ouoba, L. I. I., C. Parkouda, B. Diawara, C. Scotti, and A. H. Varnam. 2008. Identification of Bacillus spp. from Bikalga, fermented seeds of Hibiscus sabdariffa: Phenotypic and genotypic characterization. *Journal of Applied Microbiology* 104 (1):122–31.
- Ouoba, L. I. I., K. B. Rechinger, V. Barkholt, B. Diawara, A. S. Traore, and M. Jakobsen. 2003. Degradation of proteins during the fermentation of African locust bean (Parkia biglobosa) by strains of Bacillus subtilis and Bacillus pumilus for production of Soumbala. *Journal of Applied Microbiology* 94 (3):396–402. doi: [10.1046/j.1365-2672.2003.01845.x](https://doi.org/10.1046/j.1365-2672.2003.01845.x).
- Owens, J. D., N. Allagheny, G. Kipping, and J. M. Ames. 1997. Formation of volatile compounds during Bacillus subtilis fermentation of soya beans. *Journal of the Science of Food and Agriculture* 74 (1):132–40. doi: [10.1002/\(SICI\)1097-0010\(199705\)74:1<132::AID-JSFA779>3.0.CO;2-8](https://doi.org/10.1002/(SICI)1097-0010(199705)74:1<132::AID-JSFA779>3.0.CO;2-8).
- Pant, G., A. Prakash, J. V. P. Pavani, S. Bera, G. V. N. S. Deviram, A. Kumar, M. Panchpuri, and R. G. Prasuna. 2015. Production, optimization and partial purification of protease from Bacillus subtilis. *Journal of Taibah University for Science* 9 (1):50–5. doi: [10.1016/j.jtusci.2014.04.010](https://doi.org/10.1016/j.jtusci.2014.04.010).
- Pariza, M. W., K. O. Gillies, S. F. Kraak-Ripple, G. Leyer, and A. B. Smith. 2015. Determining the safety of microbial cultures for consumption by humans and animals. *Regulatory Toxicology and Pharmacology : RTP* 73 (1):164–71. doi: [10.1016/j.yrtph.2015.07.003](https://doi.org/10.1016/j.yrtph.2015.07.003).
- Parkouda, C., B. Diawara, and K. Debrah. 2014. Enzyme profiles of potential starter cultures for the fermentation of baobab seeds. *African Journal of Food Science* 8:249–52.
- Parkouda, C., F. Ba, L. Ouattara, K. Tano-Debrah, and B. Diawara. 2015. Biochemical changes associated with the fermentation of baobab seeds in Maari: An alkaline fermented seeds condiment from western Africa. *Journal of Ethnic Foods* 2 (2):58–63. doi: [10.1016/j.jef.2015.04.002](https://doi.org/10.1016/j.jef.2015.04.002).
- Parkouda, C., D. S. Nielsen, P. Azokpota, L. I. I. Ouoba, W. K. Amoa-Awua, L. Thorsen, J. D. Hounhouigan, J. S. Jensen, K. Tano-Debrah, B. Diawara, et al. 2009. The microbiology of alkaline-fermentation of indigenous seeds used as food condiments in Africa and Asia. *Critical Reviews in Microbiology* 35 (2):139–56. doi: [10.1080/10408410902793056](https://doi.org/10.1080/10408410902793056).
- Parkouda, C., L. Thorsen, C. S. Compaoré, D. S. Nielsen, K. Tano-Debrah, J. S. Jensen, B. Diawara, and M. Jakobsen. 2010. Microorganisms associated with Maari, a Baobab seed fermented product. *International Journal of Food Microbiology* 142 (3):292–301. doi: [10.1016/j.jfoodmicro.2010.07.004](https://doi.org/10.1016/j.jfoodmicro.2010.07.004).
- Peter-Ikechukwu, A. I., Ngozi, O. Kabuo, Serah, O. Alagbaoso, Njideka, E. Njoku, Chioma, N. Eluchie, and W. O. Momoh. 2016. Effect of wrapping materials on physico-chemical and microbiological qualities of fermented melon seed (Citrullus colocynthis L.) used as condiment. *Am. J. Food Sci. Technol* 4:14–9.
- Qian, Y., C. K. Kando, L. Thorsen, N. Larsen, and L. Jespersen. 2015. Production of autoinducer-2 by aerobic endospore-forming bacteria isolated from the West African fermented foods. *FEMS Microbiology Letters* 362 (22):fnv186. doi: [10.1093/femsle/fnv186](https://doi.org/10.1093/femsle/fnv186).
- Rantsiou, K., and L. Cocolin. 2006. New developments in the study of the microbiota of naturally fermented sausages as determined by molecular methods: A review. *International Journal of Food Microbiology* 108 (2):255–67. doi: [10.1016/j.jfoodmicro.2005.11.013](https://doi.org/10.1016/j.jfoodmicro.2005.11.013).
- Sanni, A. I., A. Onilude, I. Fadahunsi, S. Ogunbanwo, and R. Afolabi. 2002. Selection of starter cultures for the production of ugba, a fermented soup condiment. *European Food Research and Technology* 215 (2):176–80. doi: [10.1007/s00217-002-0520-3](https://doi.org/10.1007/s00217-002-0520-3).
- Sanni, A. I., G. S. Ayerno, E. Sakyi-Dawson, and S. Sefa-Dedeh. 2000. Aerobic spore-forming bacteria and chemical composition of some Nigerian fermented soup condiments. *Plant Foods for Human Nutrition (Dordrecht, Netherlands)* 55 (2):111–8. doi: [10.1023/A:1008147120526](https://doi.org/10.1023/A:1008147120526).
- Sanni, I. A., S. Ahrne, and A. A. Onilude. 1995. Production of α -galactosidase by Lactobacillus plantarum isolated from diverse sources. *Journal of Basic Microbiology* 35 (6):427–32. doi: [10.1002/jobm.3620350610](https://doi.org/10.1002/jobm.3620350610).
- Sarkar, P. K., L. J. Jones, G. S. Craven, and S. M. Somerset. 1997. Oligosaccharide profiles of soybeans during kinema production. *Letters in Applied Microbiology* 24 (5):337–9. doi: [10.1046/j.1472-765X.1997.00035.x](https://doi.org/10.1046/j.1472-765X.1997.00035.x).
- Sarkar, P. K., and J. P. Tamang. 1995. Changes in the microbial profile and proximate composition during natural and controlled fermentations of soybeans to produce kinema. *Food Microbiology* 12:317–25. doi: [10.1016/S0740-0020\(95\)80112-X](https://doi.org/10.1016/S0740-0020(95)80112-X).
- Savadogo, A., A. Tapi, M. Chollet, B. Wathelet, A. S. Traoré, and P. Jacques. 2011. Identification of surfactin producing strains in Soumbala and Bikalga fermented condiments using polymerase chain reaction and matrix assisted laser desorption/ionization-mass spectrometry methods. *International Journal of Food Microbiology* 151 (3):299–306. doi: [10.1016/j.jfoodmicro.2011.09.022](https://doi.org/10.1016/j.jfoodmicro.2011.09.022).
- Skandamis, P. N., and G.-J. E. Nychas. 2012. Quorum sensing in the context of food microbiology. *Applied and Environmental Microbiology* 78 (16):5473–82. doi: [10.1128/AEM.00468-12](https://doi.org/10.1128/AEM.00468-12).
- Stachelhaus, T., H. D. Mootz, and M. A. Marahiel. 2002. Assembly of peptide antibiotics on modular protein templates. In *Bacillus subtilis and its closest relatives*, Sonenshein A, Losick R, Hoch J (eds), 415–435. Washington: ASM Press.

- Steinkraus, K. H. 1997. Classification of fermented foods: Worldwide review of household fermentation techniques. *Food Control* 8 (5-6): 311–7. doi: [10.1016/S0956-7135\(97\)00050-9](https://doi.org/10.1016/S0956-7135(97)00050-9).
- Stenfors Arnesen, L. P., A. Fagerlund, and P. E. Granum. 2008. From soil to gut: *Bacillus cereus* and its food poisoning toxins. *FEMS Microbiology Reviews* 32 (4):579–606. doi: [10.1111/j.1574-6976.2008.00112.x](https://doi.org/10.1111/j.1574-6976.2008.00112.x).
- Taga, M. E., and B. L. Bassler. 2003. Chemical communication among bacteria. *Proceedings of the National Academy of Sciences* 100 (Supplement 2):14549–54. doi: [10.1073/pnas.1934514100](https://doi.org/10.1073/pnas.1934514100).
- Terlabie, N. N., E. Sakyi-Dawson, and W. K. Amoa-Awua. 2006. The comparative ability of four isolates of *Bacillus subtilis* to ferment soybeans into dawadawa. *International Journal of Food Microbiology* 106 (2):145–52. doi: [10.1016/j.ijfoodmicro.2005.05.021](https://doi.org/10.1016/j.ijfoodmicro.2005.05.021).
- Thorsen, L., P. Azokpota, B. M. Hansen, D. J. Hounhouigan, and M. Jakobsen. 2010. Identification, genetic diversity and cereulide producing ability of *Bacillus cereus* group strains isolated from Beninese traditional fermented food condiments. *International Journal of Food Microbiology* 142 (1-2):247–50. doi: [10.1016/j.ijfoodmicro.2010.06.004](https://doi.org/10.1016/j.ijfoodmicro.2010.06.004).
- Thorsen, L., P. Azokpota, B. Munk Hansen, M. H. Rønsbo, K. F. Nielsen, D. J. Hounhouigan, and M. Jakobsen. 2011. Formation of cereulide and enterotoxins by *Bacillus cereus* in fermented African locust beans. *Food Microbiology* 28 (8):1441–7. doi: [10.1016/j.fm.2011.07.003](https://doi.org/10.1016/j.fm.2011.07.003).
- Uzeh, R. E., R. E. Ohenhen, and A. K. Rojgubokan. 2006. Microbiological and nutritional qualities of dairy products: Nono and Wara. *Nature and Science* 4 (3):37–40.
- Wang, J., and D. Y. Fung. 1996. Alkaline-fermented foods: A review with emphasis on pidan fermentation. *Critical Reviews in Microbiology* 22 (2):101–38. doi: [10.3109/10408419609106457](https://doi.org/10.3109/10408419609106457).
- Waters, C. M., and B. L. Bassler. 2005. Quorum sensing: Cell-to-cell communication in bacteria. *Annual Review of Cell and Developmental Biology* 21:319–46. doi: [10.1146/annurev.cellbio.21.012704.131001](https://doi.org/10.1146/annurev.cellbio.21.012704.131001).
- Williams, P., K. Winzer, W. C. Chan, and M. Camara. 2007. Look who's talking: Communication and quorum sensing in the bacterial world. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 362 (1483):1119–34. doi: [10.1098/rstb.2007.2039](https://doi.org/10.1098/rstb.2007.2039).
- Winzer, K., K. R. Hardie, N. Burgess, N. Doherty, D. Kirke, M. T. G. Holden, R. Linforth, K. A. Cornell, A. J. Taylor, P. J. Hill, et al. 2002. LuxS: Its role in central metabolism and the in vitro synthesis of 4-hydroxy-5-methyl-3(2H)-furanone. *Microbiology (Reading, England)* 148 (Pt 4):909–22. doi: [10.1099/00221287-148-4-909](https://doi.org/10.1099/00221287-148-4-909).
- Wise, C., L. Novitsky, A. Tsopmo, and T. J. Avis. 2012. Production and antimicrobial activity of 3-hydroxypropionaldehyde from *Bacillus subtilis* strain CU12. *Journal of Chemical Ecology* 38 (12): 1521–7. doi: [10.1007/s10886-012-0219-2](https://doi.org/10.1007/s10886-012-0219-2).
- Xie, M., J. Wu, F. An, X. Yue, D. Tao, R. Wu, and Y. Lee. 2019. An integrated metagenomic/metaproteomic investigation of microbiota in dajiang-meju, a traditional fermented soybean product in Northeast China. *Food Research International (Ottawa, Ont.)* 115: 414–24. doi: [10.1016/j.foodres.2018.10.076](https://doi.org/10.1016/j.foodres.2018.10.076).
- Zhang, P., R. Wu, P. Zhang, Y. Liu, D. Tao, X. Yue, Y. Zhang, J. Jiang, and J. Wu. 2018. Structure and diversity of bacterial communities in the fermentation of da-jiang. *Annals of Microbiology* 68 (8):505–12. doi: [10.1007/s13213-018-1355-x](https://doi.org/10.1007/s13213-018-1355-x).
- Zhang, Y. C., Venkitasamy, Z. Pan, W. Liu, and L. Zhao. 2017. Novel umami ingredients: Umami peptides and their taste. *Journal of Food Science* 82 (1):16–23. doi: [10.1111/1750-3841.13576](https://doi.org/10.1111/1750-3841.13576).