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REVIEW
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Plant-Based Alkaline Fermented Foods as Sustainable Sources of Nutrients and Health-Promoting Bioactive Compounds

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Traditional food fermentation is a practice that precedes human history. Acidic products such as yogurts and sourdoughs or alcoholic beverages produced through lactic acid or yeast fermentations, respectively, are widely described and documented. However, a relatively less popular group of fermented products known as alkaline fermented foods are common traditional products in Africa and Asia. These products are so called "alkaline" because the pH tends to increase during fermentation due to the formation of ammonia resulting from protein degradation by *Bacillus* species. Plant-based alkaline fermented foods (AFFs) are generally produced from legumes including soybean, non-soybean leguminous seeds, and other non-legume plant raw materials. Alkaline fermented food products such as *natto*, *douchi*, *kinema*, *doenjang*, *chongkukjang*, *thua nao*, *meitauza*, *yandou*, *dawadawa/iru*, *ugba*, *kawal*, *okpehe*, *otiru*, *oso*, *ogiri*, *bikalga*, *maari/tayohounta*, *ntoba mbodi*, *cabuk*, and *owoh* are produced at small industrial scale or household levels and widely consumed in Asia and Africa where they provide essential nutrients and health-promoting bioactive compounds for the population. Alkaline food fermentation is important for sustainable food security as it contributes to traditional dietary diversity, significantly reduces antinutritional components in raw plant materials thereby improving digestibility, improves health *via* the production of vitamins, and may confer probiotic and post-biotic effects onto consumers. In this review, we present currently available scientific information on plant-based AFFs and their role as sustainable sources of nutrients and bioactive compounds for improved health. Finally, we provide perspectives on research needs required to harness the full potential of AFFs in contributing to nutrition and health.

Keywords: sustainability, *Bacillus spp*., nutrition, legume, fermentation, Africa, Asia

OVERVIEW OF TRADITIONAL ALKALINE FERMENTED FOODS

Food fermentation is a practice that precedes human history and will continue to be with us far into the future as populations around the world today obtain a considerable portion of their nutritional needs and incomes through fermented foods processing (Hesseltine and Wang, 1980; Tamang et al., 2020). When applied to foods, fermentation has a much broader meaning as opposed the strict biochemical definition of "an ATP-generating process in which organic compounds act as both donors and acceptors of electrons" (Kim et al., 2012). Thus, fermented foods and beverages include "foods that are made through desired microbial growth and enzymatic conversions of food components" (Marco et al., 2021). It is estimated that over 5,000 varieties of fermented foods and beverages are produced and consumed around the world from diverse raw materials (substrates) such as cereals, roots and tubers, meat, dairy products, fish, fruits, vegetables and legumes (Owusu-Kwarteng et al., 2012, 2020; Akabanda et al., 2013; Tamang et al., 2016a, 2020; Agyei et al., 2020).

Traditional fermented foods and their associated microbes are diverse depending on the substrate and the methods used for the fermentations. Whether they are produced by uncontrolled natural fermentation or with controlled starter cultures, fermented foods attain their characteristic taste, flavor, consistency, improved nutritional, and functional properties through the effects of microbial assimilation, metabolites production, and enzymatic activities (Owusu-Kwarteng et al., 2015, 2020; Marco et al., 2021). Microbial communities in natural (spontaneous) fermented foods are principally determined by dispersal and selection. Thus, in traditional spontaneous fermentation of foods, naturally occurring autochthonous microorganisms adapt to the complex food substrate and the fermentation environment leading to competitive selection of the microbial species that are more effectively adapted and positively respond to the *in-situ* conditions (Ouoba et al., 2007; Illeghems et al., 2012; Walsh et al., 2016; Einson et al., 2018). Consequently, an active change in the microbial community and metabolic profile gets established, leading to a stable fermented food ecosystem with characteristic microbiota structure and composition, metabolome, organoleptic properties, and nutritional and health benefits (Giraffa, 2004; Wolfe and Dutton, 2015; Marco et al., 2021). However, the desired outcomes and final properties of fermented foods do not only depend on the microbial-led conversion of substrates but also on a range of physicochemical parameters such as water activity, temperature, pH, oxidation-reduction potential and substrate accessibility. Therefore, effective management of both the intrinsic and extrinsic parameters during fermentation is critical in achieving the desired characteristics and final properties of fermented food products (Terefe and Augustin, 2020).

Throughout the world, lactic acid fermented products such as yogurts and sourdoughs, acetic acid fermented vinegar or alcoholic beverages produced by lactic acid bacteria, acetic acid bacteria or yeast fermentations, respectively, are widely described and their suggested nutritional and health benefits documented. This has contributed, in part, to consumer interest and the popularity of these fermented food products (Dimidi et al., 2019; Staudacher and Nevin, 2019). However, a relatively less popular yet rich diverse group of fermented products known as alkaline fermented foods (AFFs) which form an essential part of the diets and culture of people in parts of Africa and Asia (Ouoba et al., 2004; Azokpota et al., 2006; Parkouda et al., 2009; Owusu-Kwarteng et al., 2020; Tamang et al., 2020) have received relatively little attention. **Figure 1** shows a comparison of studies published on the Scopus database with the terms "lactic acid fermentation" and "alkaline fermentation" in title, abstract or keywords. Active research in the area of "alkaline food fermentation" only began to "take off" in the late 1980s, whereas lactic acid fermentation had benefited from detailed scientific research dated as far back as in 1950. Indeed, pioneering scientific research on African alkaline fermented foods only started in 1980s with the microbiology works on *iru* (Odunfa, 1981), *dawadawa* (Campbell-Platt, 1980), *ogiri* (Odunfa, 1983, 1985), and *ugba* (Odunfa and Oyewole, 1986).

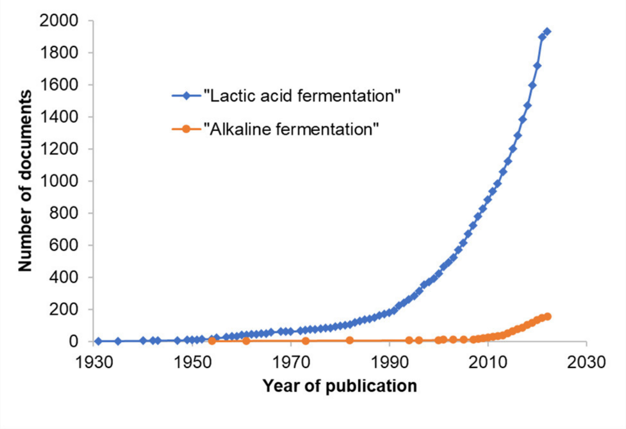

FIGURE 1 | Comparison of cumulative publication outputs in Scopus database on the search terms "lactic acid fermentation" and "alkaline fermentation" (Search done on 23rd February 2022).

These so called "alkaline fermented foods" tends to have their pH increasing during fermentation. Thus, the predominant *Bacillus* spp. in these alkaline fermentations degrade the endogenous proteins in the raw plant into peptides and amino acids (Odunfa, 1985; Ouoba et al., 2003). As shown in equation 1, the free amino acids are further utilized by the *Bacillus* spp. as carbon and nitrogen sources to produce ammonia/ammonium hydroxide, resulting in the high pH values and the associated atypical odor of these fermented condiments (Ouoba et al., 2003, 2005; Parkouda et al., 2009; Amoa-Awua et al., 2014).

$$RCH(NH_3^+)COO^- + nO_2 \rightarrow nCO_2 + nH_2O + NH_4^+ + OH^-$$

AFFs of Africa and Asia are produced from a range of protein-rich substrates such as *Glycine max* (soybeans), *Parkia biglobosa* (African locust bean) seeds and other non-leguminous plant parts. Plant-based AFFs of Asia are almost exclusively produced

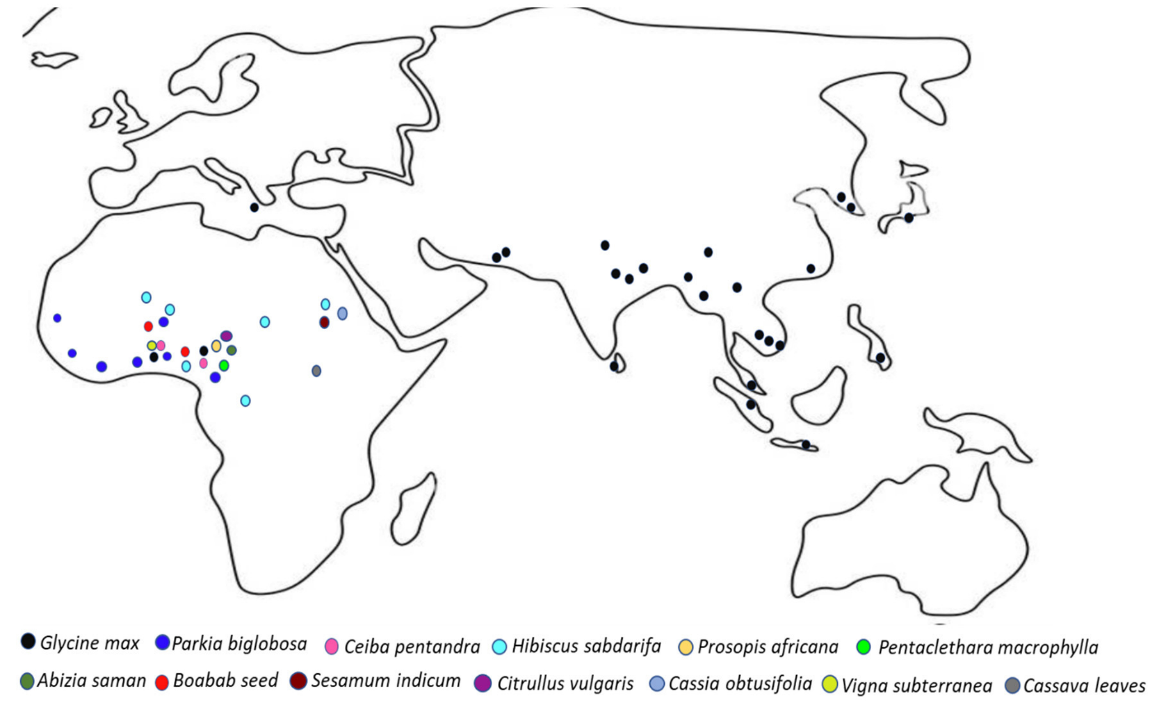

FIGURE 2 | Diversity and distribution of plant species used for the production of alkaline fermented foods in Africa and Asia.

from soybean as the substrate, giving credence to the first domestication of soybean in Asia particularly in the eastern half of north China in 1,000 BC, and the importance and agricultural sustainability of soybean across the Asian region (Tamang et al., 2020). In Africa, however, several wild as well as cultivated legumes and non-leguminous plants are used as substrates to produce AFFs. Asian AFFs produced from soybean include *natto* from Japan (Kanno and Takamatsu, 1987), *douchi* from China (Fan et al., 2009), *kinema* and similar products from Nepal and neighboring countries such as Bengal, India, and Bhutan (Tamang et al., 2002), *doenjang* and *chongkukjang* from Korea (Park, 2000; Kim, 2002; Park and Jung, 2005; Baek et al., 2008; Park et al., 2010), *thua nao* from Thailand (Leejeerajumnean, 2000), and *meitauza* and *yandou* from China (Zhu et al., 2008; Xu et al., 2012; Qin et al., 2013). On the other hand, African locust bean [*Parkia biglobosa* (Jacq. Benth)] is a common substrate for AFF condiments in Africa under different local names such as *dawadawa* in Ghana and Nigeria, *soumbala* in Burkina Faso (Ouoba et al., 2004), *afitin*, *iru* or *sonru* in Benin (Azokpota et al., 2006), *nététou* in Senegal (N'Dir et al., 1994), *kinda* in Sierra Leone and *iru* among the Yoruba tribe of Southwestern Nigeria (Sanni et al., 2000). Similarly, roselle seeds [*Hibiscus sabdariffa* (Linn.)] is used to produce AFF condiment such as *bikalga* in Burkina Faso (Ouoba et al., 2008), *yanyanku* and *ikpiru* in Benin (Agbobatinkpo et al., 2013) and *mbuja* in Cameroon (Mohamadou et al., 2013). Other plant based AFFs in Africa include *okpehe* from *Prosopis africana* seeds (Achi, 1992; Oguntoyinbo et al., 2010), *otiru* from African yam bean (Jeff-Agboola, 2007), *oso* from *Cathormion altissimum* seeds (Popoola et al., 2004), *ugba* from *Pentaclethra macrophylla* seeds (Sanni et al., 2002; Ahaotu et al., 2013), *maari* and *tayohounta* from Baobab seed (Parkouda et al., 2010; Chadare et al., 2011; Kaboré et al., 2012), *ogiri* from melon/castor oil seeds (Odunfa, 1985; Ademola et al., 2018), *owoh* from cotton seeds (*Gossypium hirsutum*) seeds (Sanni and Ogbonna, 1991; Ezekiel et al., 2015), *mantchoua* and *kantong* from Kapok tree (*Ceiba pentadra*) seed (Kpikpi et al., 2014; Kere-Kando et al., 2020) and *ntoba mbodi* from cassava leaves (Louembe et al., 2003; Mbozo et al., 2017; Moutou-Tchitoula et al., 2018). A range of plant species used for the processing of AFFs in Asia and Africa are shown in **Figure 2**.

Being predominantly produced from locally cultivated and wild plants, AFFs and the microorganisms therein provide sustainable diets serving as sources of nutrients and health promoting bioactive molecules thereby contributing toward achieving the United Nations Sustainable Development Goals (SGD), specifically SGDs 2 and 3. In addition to the general benefits associated with fermentation such as improvement in shelf-life, organoleptic quality and safety, alkaline food fermentations play a significant role in nutritional intake of several traditional communities in Africa and Asia where these fermentation processes transforms somewhat inedible, unpalatable, potentially toxic and undigestible plant materials into diverse desirable food products that delivers essential nutrients such as proteins, amino acids, vitamins and minerals within otherwise marginal diets (Wang and Fung, 1996; Parkouda et al., 2009; Reddy et al., 2018). Furthermore, AFFs and their associated microorganisms have been associated with several putative health-promoting effects that can positively impact human health *via* mechanisms such as including nutritive alteration of raw components, biosynthesis of bioactive compounds, modification of the human gut microbiota, and development and modification of the immune system (Shin et al., 2001; Sarkar et al., 2002; Hosoi et al., 2003; Suzuki et al., 2004; Zhang et al., 2006; Wang et al., 2008; Tolhurst et al., 2012; Tamang et al., 2016a; Araki et al., 2020). However, except for *natto* which has received at least one Randomized Control Trial (RCT), evidence of nutritional and health promoting effects of AFFs or their inherent microorganisms have so far been limited to laboratory chemical analysis and animal/cell model studies in contrast to other fermented foods such as yogurts and cultured milk which have their health benefits reported through at least 20 RTCs for both healthy and patient population groups (Dimidi et al., 2019; Araki et al., 2020; PraŽnikar et al., 2020; Savaiano and Hutkins, 2021). In this review, we demonstrate based on reported scientific information, the potential contribution of plant-based AFFs toward achieving the UN-SDGs as these foods serve as a sustainable source of healthy and nutritious diets for many traditional communities in Africa and Asia. Finally, we present future perspective on the need to apply holistic, meta-omics methods (metagenomics, meta-transcriptomics, meta-proteomics and metabolomics) to characterize traditional AFFs as well as conduct properly designed large placebo-controlled RCTs that will provide a better understanding of the health benefits of traditional AFFs.

PREDOMINANT MICROORGANISMS IN AFF*s*

In order to appreciate the scope of AFFs in nutrition and health, it is necessary to acknowledge the diversity and origin of predominant microorganisms responsible for the fermentation of these products. In general, traditional AFFs of Africa and Asia are processed by spontaneous fermentation (depends on autochthonous or resident microorganism present in the raw substrate and/or surrounding environment) to initiate the fermentation processes in these products (Parkouda et al., 2009; Owusu-Kwarteng et al., 2020; Tamang et al., 2020). In assessing their microbial ecology, the gold standard culture dependent phenotypic approaches complemented by molecular tools such as internal transcribed spacer PCR (ITS-PCR), random amplification polymorphic DNA-PCR (RAPD-PCR), repetitive sequence-based PCR (rep-PCR), pulsed field gel electrophoresis (PFGE), as well as sequencing of 16S rRNA, *gyrA*, *gyrB*, and *rpoB* genes, have shown that plant-based AFFs of Africa and Asia are characterized by complex microbial communities. Despite this complexity, *Bacillus subtilis* and related species are the predominant functional microbiota in a wide-range of plant-based AFFs of Africa and Asia (Ouoba et al., 2004, 2010; Meerak et al., 2007, 2008; Oguntoyinbo et al., 2007; Parkouda et al., 2009, 2010; Chukeatirote et al., 2010; Kamada et al., 2015; Owusu-Kwarteng et al., 2020). Predominant microbial species associated with the fermentation of plant-based AFFs in Asia and Africa are shown in **Table 1**. Frequently identified species of *Bacillus* and related genera associated with plant-based AFFs are *Bacillus subtilis*, *Bacillus cereus*, *Bacillus megaterium*, *Bacillus endophyticus*, *Bacillus licheniformis*, *Bacillus borstelensis*, *Bacillus pumilus*, *Bacillus coagulans*, *Bacillus circulans*, *Paenibacillus polymyxa*, *Lysinibacillus sphaericus*, and *Lysinibacillus fusiformis* (Odunfa, 1981; Sarkar et al., 2002; Ouoba et al., 2004, 2010; Azokpota et al., 2007; Parkouda et al., 2009).

Irrespective of raw material or geographic location of production, *B. subtilis* remains the dominant functional species in most AFFs in Africa and Asia. *B. subtilis* is reported as the predominant species in the fermentation of *dawadawa* and *soy-daddawa* in Ghana and Nigeria (Dakwa et al., 2005; Amoa-Awua et al., 2006; Ezeokoli et al., 2016), *soumbala, bikalga*, *maari* and *mantchoua* in Burkina-Faso (Bengaly, 2001; Ouoba et al., 2004, 2007, 2010; Parkouda et al., 2010; Kaboré et al., 2012; Kere-Kando et al., 2020), *kawal* in Sudan and Chad (Mbaiguinam et al., 2005), *soumbara* in Côte d'Ivoire (Adjoumani et al., 2019), *afitin*, *sonru*, and *iru* in Benin (Azokpota et al., 2007), *tayohounta*, *yanyanku,* and *ikpiru* in Benin (Chadare et al., 2011; Agbobatinkpo et al., 2013), *mbuja* in Cameroon (Mohamadou et al., 2013), *kinda* in Sierra Leone (Meerak et al., 2008), and *okpehe*, *oso*, *ugba*, *iru*, and *owoh* in Nigeria (Sanni et al., 2000, 2002; Popoola et al., 2004; Oguntoyinbo et al., 2010; Adewumi et al., 2013, 2014; Ahaotu et al., 2013; Ezekiel et al., 2015; Ademola et al., 2018). Similarly, Asian AFFs produced from soybean such as *kinema* produced in Nepal, *thua nao* in Thailand, *chongukukjang* and *doenjang* in Korea, *meitauza* in China, and *natto* in Japan are produced by *B. subtilis* (Tamang et al., 2016b).

The *B. subtilis* species complex is a tight assemblage of related species that includes *B. subtilis* subsp. *subtilis* BEST195, the starter strain used for *natto* fermentation which is thought to have been isolated from a traditionally prepared *natto* and was therefore originally named *Bacillus natto*. However, *Bacillus natto* was re-classified and included in *B. subtilis* in 1970 supported by phylogenetic analyses using 16S rRNA genes (Tamang et al., 2002; Kubo et al., 2011). Since its isolation, further characterization including entire genome information (Kiuchi et al., 1987; Sulistyo et al., 1988; Nishito et al., 2010) have led to the development of *B. subtilis* subsp. *subtilis* BEST195 starter strain used for natto production in Japan. *Natto* starter cultivation generally targets genes regulating the metabolic pathways of secondary metabolites that affect texture, aroma, sensitivity to bacteriophages, spore formation and germination, and high productivity of ϒPGA *via* the *pgs* operon (Ashiuchi and Misono, 2002; Beckett, 2009; Kubo et al., 2011) which imparts a sticky texture onto *natto*. In plant-based African AFFs, *B. subtilis* play technological and functional roles such as Production of Aroma/flavor compounds (Owens et al., 1997; Ouoba et al., 2005; Nwokeleme and Ugwuanyi, 2015; Akanni et al., 2018), amino acids synthesis (Ouoba et al., 2003; Azokpota et al., 2006), degradation of carbohydrates and oils (Kiers et al., 2000; Ouoba et al., 2003, 2007; Azokpota et al., 2006), production of antimicrobial peptides (Ouoba et al., 2007; Savadogo et al., 2011; Kaboré et al., 2012, 2013; Compaore et al., 2013), and reduction of anti-nutritional factors and toxic compounds (Okafor, 1977; Odunfa, 1985; Abban et al., 2013).

Being produced predominantly by spontaneous fermentation processes, the microbial ecology of traditional plant-based AFFs of Africa and Asia are generally characterized by mixed

TABLE 1 | Overview of predominant microorganisms occurring in plant-based AFFs in Africa and Asia.

Product name	Substrate/raw material	Predominant microorganisms	Method of identification	Country/region	References
Legume; soybean products					
Aakhone	Soybean	*B. subtilis, B. licheniformis, B. cereus, Staphy. Epidermis, Proteus mirabilis, Alcaligenes faecalis*	Phenotypic tests, 16S rRNA sequence	India	Singh et al., 2014; Jamir and Deb, 2018
Bekang	Soybean	*B.subtilis, B.brevis, B.circulans, B.coagulans, B. licheniformis, B. pumilus, B. sphaericus, L. fusiformis*	Phenotypic tests, ARDRA, ITS-PCR, and RAPD-PCR	India	Chettri and Tamang, 2015; Tamang et al., 2016a
Chongkukjang (also written as Chungkukjang)	Soybean	*B subtilis, B.amyloliquefaciens, B.licheniformis, B. cereus, Pantoea agglomerans, Pantoega ananatis, Enterococcus sp., Pseudomonas sp., Rhodococcus sp.*	Culture-based, DGGE, barcoded pyrosequencing, RAPD-PCR	Korea	Lee et al., 2010; Hong et al., 2012; Nam et al., 2012; Shin and Jeong, 2015
Douchi	Soybean	*B. amyloliquefaciens, Pediococcus acidilactici, P. pentosaceus, L. brevis, L. plantarum, S. cerevisiae, M. farinosa (formerly Pichia farinosa), C. guilliermondii, A. oryzae Absidia corymbifera, D. hansenii, C. guilliermondii, C. variabilis*	DGGE and sequencing of excised PCR products	China	Peng et al., 2003; Parkouda et al., 2009; Chen et al., 2011a,b, 2012; Liu et al., 2012; Qu et al., 2012
Doenjang	Soybean	*B. subtilis, B. licheniformis, Staphy. equorum, E. durans, E. faecium, Leuco. mesenteroides, Tetragenococcus halophilus, Absidia corymbifera, A. corymbifera, A. oryzae, Mucor plumbeus, Debaryomyces hansenii, Candida rugose, D. hansenii, Zygo. rouxii, G. geotrichum, C. pelliculosa (formerly Pichia anomala/Hansenula anomala), Pichia farinose, Sterigmatomyces halophilus*	Phenotypic tests, DGGE and sequencing, PCR-DGGE, pyrosequencing of 16S rRNA genes sequencing	Korea	Yoo et al., 1999; Kang et al., 2000; Cho and Seo, 2007; Kim et al., 2009; Lee et al., 2010; Nam et al., 2012; Shin and Jeong, 2015
Furu	Soybean curd	*B. pumilus, B. megaterium, B. stearothermophilus, B. firmus, Staph. hominis*	Phenotypic tests, PCR	China	Sumino et al., 2003; Tamang et al., 2016a
Gochujang/Kochujang	Soybean, red pepper	*B. velezensis, B. amyloliquefaciens, B. subtilis, B. licheniformis, B. velezensis, Zygo. rouxii, C. apicola, Z. beilli*	Phenotypic tests, PCR	Korea	Shin and Jeong, 2015
Hawaijar	Soybean	*B. subtilis, B. licheniformis, B. amyloliquefaciens, B. cereus, Staph. aureus, Staph. sciuri, Alkaligenes sp., Providencia rettgers, Proteus mirabilis*	Phenotypic tests, ARDRA, PCR amplification of 16S-23S rDNA region, RAPD-PCR, RFLP	India	Jeyaram et al., 2008; Singh et al., 2014; Tamang et al., 2016a
Kanjang	Soybean	*Bacillus citreus, B. circulans, B. licheniformis, B. megaterium, B. mesentricus, B. subtilis, B. pumilis, Lactobacillus sp., Pedicocus sp., P. acidilactici, A.s oryzae*	Phenotypic tests, PCR	Korea	Shin and Jeong, 2015
Kinema	Soybean	*B. subtilis, E. faecium, C. parapsilosis, G. candidum, B. licheniformis, B. cereus, B. circulans, B. thuringiensis, B. sphaericus*	RAPD-PCR	Nepal, Bhutan, Bengal	Sarkar et al., 1994, 1997a,b, 2002; Sarkar and Tamang, 1995; Kiers et al., 2000; Dahal et al., 2005; Parkouda et al., 2009
Thua nao	Soybean	*B. subtilis, B. licheniformis, B. megaterium, B. pumilus, Lactic acid bacteria*	Phenotypic test, randomly amplified polymorphic DNA-PCR fingerprinting, 16S rRNA gene sequencing	Thailand	Chantawannakul et al., 2002; Visessanguan et al., 2005; Inatsu et al., 2006; Chukeatirote, 2015; Pakwan et al., 2020

(Continued)

TABLE 1 | Continued

Product name	Substrate/raw material	Predominant microorganisms	Method of identification	Country/region	References
Tungrymbai	Soybean	*B. licheniformis, B. pumilus B. subtilis*	Phenotypic tests, ARDRA, ITS-PCR, and RAPD-PCR	India	Chettri and Tamang, 2015
Meitauza	Soybean	*B. subtilis, Actinomucor elegans*, *Zymomonas mobilis*		China	Kronenberg and Hang, 1984; Xu et al., 2012
Natto	Soybean	*B. subtilis* var natto	16S rRNA genes sequencing	Japan	Tamang et al., 2002; Kiuchi and Watanabe, 2004; Kubo et al., 2011
Peruyaan	Soybean	*B. subtilis, B. amyloliquefaciens, Vagococcus lutrae, P. acidilactici, E. faecalis*		India	Singh et al., 2014
Yandou	Soybean	*B. subtilis* subsp. *Subtilis, B. licheniformis, B. amyloliquefaciens*	454 pyrosequencing of 16S rRNA genes sequencing	China	Qin et al., 2013
Sere kedele	Soybean	*B. cereus B. flexus, B. subtilis, B. thuringiensis, W. confusa, W. cibaria, Acinetobacter baumannii, Proteus mirabilis, Klebsiella pneumoniae*	Phenotypic tests, 16S rRNA gene sequencing	Indonesia	Suparthana et al., 2018
Soy-daddawa	Soybean	*B. subtilis, B. licheniformis, B. pumilus, B. cereus, B. firmis, M. luteus, Staphy epidermidis*	Phenotypic, PCR-DGGE and 16S rRNA gene sequencing	Nigeria	Dakwa et al., 2005; Amoa-Awua et al., 2006; Terlabie et al., 2006; Ezeokoli et al., 2016
Tungrymbai	Soybean	*B. subtilis, B. licheniformis, B. pumilus*	ARDRA, ITS-PCR and RAPD-PCR techniques	India	Chettri and Tamang, 2015
Legume; non-soybean products					
Afitin, *sonru*, and *iru*	*Parkia biglobosa* seed	*B. subtilis, B. licheniformis, B. cereus*, *Staphylococcus* spp.	ITS-PCR-RFLP, 16S rRNA gene sequencing	Benin	Azokpota et al., 2007
Bhallae	Black gram (*Vigna mungo*)	*B. subtilis, Candida curvata, C. famata, C. membraneafaciens, C. variovaarai, Cryptococcus humicoius, D. hansenii, G. candidum, Hansenula anomala, H. polymorpha, K. marxianus, L. fermentum, Leuc. mesenteroides, P. membranaefaciens, R. marina, S. cerevisiae, E. faecalis, Trichosporon beigelii, Trichosporon pullulans, Wingea robertsii*		India	Tamang et al., 2016a
Dawadawa	*Parkia biglobosa* seed	*B. subtilis, B. pumilus, B. licheniformis, B. firmus, B. atrophaeus, B. amyloliquefaciens, B. mojavensis, Tetragenococcus halophilus, P. pentosaceus, L. plantarum, Lysininbacillus sphaericus. Leuconostoc spp., Staphylococcus spp., P. aeruginosa*	Phenotypic tests, 16S rRNA gene sequencing	Ghana, Nigeria	Sanni et al., 2000; Omafuvbe et al., 2004; Amoa-Awua et al., 2006; Meerak et al., 2008; Uaboi-Egbenni et al., 2009
Soumbala	*Parkia biglobosa* seed	*B. subtilis, B. pumilus, B. cereus, B. sphaericus, Brevibacillus borstelensis, B. thuringiensis, B. licheniformis, B. badius, Paenibacillus alvei, B. firmus, P. larvae, Brevibacillus laterosporus, B. megaterium, B. mycoides, E. faecium, E. hirae, P. acidilactici, L. brevis*	ITS-PCR, ITS-PCR RLFP, PFGE, 16S rRNA sequencing, RAPD-PCR fingerprint	Burkina Faso	Sarkar et al., 2002; Ouoba et al., 2004, 2010
Maseura	Black gram (*Vigna mungo*)	*B. subtilis, B. mycoides, B. pumilus, B. laterosporus, P. acidilactici, P. pentosaceous, E. durans, L. fermentum, L. salivarius, S. cerevisiae, Pic. burtonii, C. castellii*	Phenotypic tests	Nepal, India	Chettri and Tamang, 2008

(Continued)

TABLE 1 | Continued

Product name	Substrate/raw material	Predominant microorganisms	Method of identification	Country/region	References
Nététou	*Parkia biglobosa* seed	*B. licheniformis, B. coagulans, B. subtilis, B. pumilus, Staphylococcus spp. Micrococcus spp*	Phenotypic tests	Senegal	N'Dir et al., 1994; N'dir et al., 1997
Kawal	Sickle pod (*Senna obtusifolia* (L.) leaves	*B. subtilis*, *L. plantarum*, *Propionibacterium* sp., *Staphy. sciuri*, C. *krusei Saccharomyces* sp	Phenotypic tests	Sudan, Chad	Dirar, 1984; Harper and Collins, 1992; Mbaiguinam et al., 2005
Kinda	Locust bean	*B. pumilus, B. licheniformis, B. subtilis, B. atrophaeus, B.amyloliquefaciens, B.mojavensis, Lysininbacillus sphaericus*	16S rDNA sequencing	Sierra Leone	Meerak et al., 2008
Okpehe	*Prosopis africana* seeds	*B. subtilis, B. licheniformis, B. pumilus, B. megaterium, B. cereus, Staphy. epidermidis, M. luteus, E. coli, Ent. cloacae, K. pneumoniae, Lactobacillus spp., Proteus spp., Pseudomonas spp., Enterococcus spp., Staphylococcus spp., Micrococcus spp., S. cerevisiae*	Phenotyping, RAPD-PCR, ARDRA fingerprinting, 16S rRNA gene sequencing	West Africa/middle belt and southern Nigeria	Achi, 1992; Omafuvbe et al., 1999; Oguntoyinbo and Oni, 2004; Ogunshe et al., 2007; Oguntoyinbo et al., 2007, 2010; Balogun and Oyeyiola, 2011; Musa et al., 2011
Otiru	African yam bean (AYB) plant	*L. jensenii, B. coagulans, Aero. viridans, P. pentosaceus, S. cerevisiae, C. vini. A. niger, S. cerevisiae, C. vini* (formerly *Candida mycoderma)*	Phenotypic and biochemical tests	Nigeria	Jeff-Agboola, 2007
Oso	Seeds of *Cathormion altissimum* Hutch	*Bacillus subtilis, Bacillus licheniformis, Leuconostoc mesenteroides, Staphylococcus spp*		West Africa/Nigeria	Popoola et al., 2004, 2005, 2007
Ugba	*Pentaclethra macrophylla*	*B. subtilis, B. pumilus, B. licheniformis, B. brevis, B. megaterium, B. polymyxa, B. coagulans, B. macerans, B. cereus, Lactobacillus spp., Micrococcus spp., Pseudomonas chlororaphis, Micrococcus roseus, Staphyl. saprophyticus, Staphylococcus spp.*	Phenotyping, sequencing of 16S rRNA, *gyrB* and *rpoB* genes, 16S-23S rRNA ITS-PCR, and rep-PCR	Nigeria	Isu and Njoku, 1997; Mbajunwa et al., 1998; Isu and Ofuya, 2000; Sanni et al., 2000, 2002; Parkouda et al., 2009; Ahaotu et al., 2013
Iru	*Parkia biglobosa* seed	*B. subtilis*, *B. amyloliquefaciens*, *B. cereus*, *B. licheniformis, B. pumilus, Brevibacillus formosus, B. brevis, B. megaterium, B. polymyxa, Leuconostoc spp., Staphylococcus spp., Pseudomonas aeruginosa*	Phenotypic tests, ARDRA, ITS-PCR, ITS-PCR-RFLP, RAPD-PCR, PCR-DGGE, 16S rRNA gene sequencing	Nigeria	Odunfa and Oyewole, 1986; Sanni et al., 2000; Omafuvbe et al., 2004; Adewumi et al., 2013, 2014
Dawadawa-type condiment	Bambara groundnut	*B. subtilis* subsp. *subtilis, B. amyloliquefaciens* subsp. *plantarum, B. pumilus* and *B. licheniformis*	MALDI-TOF MS, 16S rRNA, and *gyr*A genes sequencing	Ghana, Nigeria	Barimalaa et al., 1994; Amadi et al., 1999; Akanni et al., 2018
Soumbara	*Parkia biglobosa* seed	*B. subtilis, B. velezensis, B. pumilis*, *E. faecium, E. hirae, Pediococcus acidilactici, L. brevis*	16S rRNA genes sequencing, RFLP analysis	Côte d'Ivoire, Burkina Faso	Ouoba et al., 2010; Adjoumani et al., 2019

(Continued)

TABLE 1 | Continued

Product name	Substrate/raw material	Predominant microorganisms	Method of identification	Country/region	References
Non-legume products					
Bikalga	*Hibiscus sabdariffa*	*B. subtilis, B. licheniformis, B. cereus, B. pumilus, B. badius, Brevibacillus bortelensis, B. sphaericus, B. fusiformis, B. amyloliquefaciens, B. sphaericus, B. coagulans, and B. firmus, B. polymyxa, B. circulans, Brevibacillus brevis, and Brevibacillus laterosporus Enterococcus faecium, Enterococcus hirae, P. acidilactici, P. pentosaceus, L. brevis, Leuc. mesenteroides subsp. dextranicum, L. bulgaricus, Staphylococcus spp.*	Phenotypic tests, 16S-23S rRNA (ITS-PCR) gene sequencing	Burkina Faso	Bengaly, 2001; Ouoba et al., 2007; Ouoba et al., 2008a, Mohamadou et al., 2008; Ouoba et al., 2010; Mohammadou et al., 2018
Maari	Baobab seed	*B. subtilis, B. licheniformis, B. velezensis, B. safensis, B. megaterium, B. endophyticus, B. cereus, B. coagulans, B. circulans, E. faecium, E. casseliflavus, P. acidilactici, Staphy. sciuri, Staphy. gallinarum, Corynebacterium sp.*	Phenotypic tests, rep-PCR $(GTG)_5$-fingerprinting and 16S rRNA gene sequencing	Burkina Faso	Parkouda et al., 2010; Kaboré et al., 2012
Ogiri	Melon/Castor oil seeds	*B. safensis, B. siamensis, B. altitudinis, B. encimensis, B. subtilis, B. circulans, B. stearothermophilus, Brevibacillus brevis, B. megaterium, L. pentosus, L. plantarum*	Phenotypic tests (API kit software), 16S rRNA gene sequencing	Nigeria	Odunfa, 1985; Ojinnaka and Ojimelukwe, 2013; Ademola et al., 2018
Owoh	Cotton seeds (*Gossypium hirsutum*)	*B. subtilis*, *B. licheniformis*, *B. pumilus*, *Staphylococcus* spp.	Phenotypic tests	Nigeria	Sanni and Ogbonna, 1991; Ezekiel et al., 2015
Semayi	Coconut fruit	*B. subtilis*, *B. licheniformis*, and *B. polymyxa*	Phenotypic tests	Indonesia	Kuswanto, 1988
Tayohounta	Baobab seed	*B. licheniformis, B. pumilus, B. subtilis, B. thermoamylovorans, B. thuringiensis, B. borstelensis, L. fermentum, Enterococcus casseliflavus, E. durans, L. agilis,P. pentosaceus, S. equinus,W. confuse, E. cloacae, E. faecium, E. italicus, Jeotgalicoccus halotolerans, K. pneumoniae, Staphy.aureus*	PCR-DGGE and cloning of 16S rRNA PCR fragments	Benin	Chadare et al., 2011
Mantchoua	Kapok tree (*Ceiba pentadra*) seed	*B. subtilis subsp. Subtilis, B. cereus sensu lato, B. amyloliquefaciens subsp. Plantarum, B. licheniformis, B. altitudinis, B. safensis*	Phenotypic tests, 16S rRNA, ITS-PCR, M13-PCR	Burkina Faso	Kere-Kando et al., 2020
Kantong	Kapok tree (*Ceiba pentadra*) seed	*B.s subtilis subsp. subtilis, B. safensis, B. amyloliquefaciens subsp. plantarum/B. methylotrophicus*	Phenotypic tests, M13-PCR; gyrA sequencing.	Ghana	Kpikpi et al., 2014
Mbuja	*Hibiscus sabdariffa*	*B. subtilis*, *B. megaterium*, *B. amyloliquefaciens*, *B. pumilus B. cereus*	Phenotypic tests, 16S rRNA, and *gyrB* genes sequencing	Cameroon	Mohamadou et al., 2013
Yanyanku	*Hibiscus sabdariffa*	*B. subtilis, B. cereus, B. amyloliquefacience, B. licheniformis, B. safensis, B. altitudinis, B. aryabhattai*, *B. flexus, B. circulans, Lysinibacillus spp, Paenibacillus spp, Brevibacillus spp, Aneurinibacillus spp*	Phenotypic tests, rep-PCR, M13-PCR, 16S rRNA, *gyr*A, *gyr*B sequencing	Benin	Agbobatinkpo et al., 2013
Ikpiru	*Hibiscus sabdariffa*	*B. subtilis*, *B. cereus*, *B. amyloliquefaciens*, *B. licheniformis*, *B. safensis*, *B. altitudinis*, *B. aryabhattai*, *B. flexus*, *B. circulans*, *Lysinibacillus spp*, *Paenibacillus spp*, *Brevibacillus spp*, *Aneurinibacillus spp*	Phenotypic tests, rep-PCR, M13-PCR, 16S rRNA, *gyr*A, and *gyr*B genes sequencing	Benin	Agbobatinkpo et al., 2013
Ntoba Mbodi	Cassava leaves	*B. macerans*, *B. subtilis*, *B. pumilus*, *Staphylococcus xylosus*, *Erwinia* spp, *E. faecium*, *E. hirae*, *E. casseliflavus*, *E. faecalis; E. avium*, *L. plantarum, P. pentosaceus*, *W. confusa*, *W. cibaria*, *Pediococcus* spp. *Staphy. sciuri*	16S rRNA gene sequencing and phylogenetic analyses	The Republic of Congo	Louembe et al., 2003; Jayani et al., 2005; Mokemiabeka et al., 2011; Moutou-Tchitoula et al., 2018

Natto (Photo credit: Chichi Wang) ***Kinema*** (Photo from Tamang et al., 2016a) ***Doenjang*** (Photo by: Maangchi)

Douchi (Photo by: Xin-Mei Feng) ***Dawadawa*** (photo by R. A. Atuna) ***Thua nao*** (Photo by puechkaset)

FIGURE 3 | Examples of traditional AFFs in Africa and Asia. **(A)** *Natto* (Photograph credit: Chichi Wang), **(B)** *Kinema* (Photograph from Tamang et al., 2016a), **(C)** Doenjang (Photograph by Maangchi), **(D)** *Douchi* (Photograph by Xin-Mei Fang), **(E)** *Dawadawa* (Photograph by R. A. Atuna), and **(F)** *Thua nao* (Photograph by puechkaset).

populations of different species of bacteria, yeasts and molds (Dirar et al., 1985; Sarkar et al., 1994; Dakwa et al., 2005; Jeff-Agboola, 2007; Parkouda et al., 2009, 2010; Sohliya et al., 2009; Ouoba et al., 2010; Kim et al., 2011a; Rashad et al., 2011; Tamang et al., 2012; Adewumi et al., 2013; Owusu-Kwarteng et al., 2020). Thus, in addition to *Bacillus* and related species, other groups of microorganisms including other aerobic endospore-forming bacteria (AEB), lactic acid bacteria (LAB), yeasts and molds have been frequently identified as members of the microbial consortia of traditional plant-based AFFs. However, the contribution of these so-called "secondary microbiota" to technological and functional properties of AFFs have been sparsely reported. Lactic acid bacterial may enhance the safety of AFFs through the production of antimicrobial compounds (Kaboré et al., 2012). Yeasts such as *Candida parapsilosis* and *Geotrichum candidum* have also been shown to significantly lower the levels of free fatty acids, while contributing to the production of free amino acids as well as enhance the formation of flavor compounds in traditional AFFs (Sarkar et al., 1996; Kim et al., 2011b; Rashad et al., 2011).

NUTRITIONAL AND DIETARY VALUE OF PLANT-BASED AFFs

Plant-based AFFs play significant roles in the nutritional intake and are important in achieving dietary sufficiency in several traditional communities where they are produced and consumed. Two main features of alkaline fermentation process are particularly significant in relation to national and dietary impacts of AFFs. Firstly, enzymes produced by predominant bacteria during alkaline fermentation hydrolyses macronutrient molecules i.e., complex carbohydrates, proteins, and fats, thereby enhancing nutrient bioavailability and digestibility of the fermented product compared with the unfermented substrate (Wang and Fung, 1996). For example, *B. subtilis* fermentation has been shown to effectively hydrolyse soybean proteins and polysaccharides, resulting in low-molecular-weight, water-soluble products that require little further degradation by gastrointestinal enzymes (Kiers et al., 2000). Secondly, enzymatic degradation during fermentation significantly reduces naturally occurring toxic components, allergens, and antinutritional components in the raw food substrate, thereby transforming otherwise inedible, difficult to digest or potentially toxic raw materials into palatable and culturally desirable food products that deliver essential nutrients. In Africa, several of such alkaline fermented food products are produced in each country or region, thus contributing to a complex rich traditional dietary diversity, with important food security and sustainability implications (Iwuoha and Eke, 1996; Parkouda et al., 2009).

Soybean, the most common plant substrate for AFFs produced in Asia, is nutritious with high levels of protein and fat (Bouchenak and Lamri-Senhadji, 2013). However, unprocessed soybean contains high levels of complex oligosaccharides and antinutrients (Reddy and Pierson, 1994), as well as potential allergens (Phromraksa et al., 2008). The presence of antinutritional factors such as tannins, trypsin inhibitors and phytic acid tend to limit the digestibility and bioavailability of essential nutrients in unprocessed soy products (Ghavidel and Prakash, 2007). Therefore, in order to liberate the essential nutrients from soybean for human digestion and absorption, some form of processing is necessary. Fermentation has proven to reduce antinutrient levels, improving the nutritional and organoleptic properties of fermented food products (Osman, 2004; Eltayeb et al., 2007; Atuna et al., 2022).

During the production of soy-based *natto* (**Figure 3A**), biochemical changes occurring as a result of fermentation has been shown to improve the content of protein, lipids and minerals such as iron, zinc and calcium (**Table 2**). Hu et al. (2010) reported 1.1-fold increase in protein content of *natto* after fermentation. It has been suggested that microorganisms increase the protein content of samples on which they grow due to microbial synthesis of protein (Hu et al., 2010). Crude fat and total ash contents of *natto* ranges from 18–24.7 to 4.7–4.6%, respectively (**Table 2**). Although fermentation is reported to have little effect on the crude fat content of natto, there appears to be strain-specific influence by the fermenting microorganism which may result in increased or decreased fat content. For example, the lipid content of natto decreased by 1.1-times from 25.41% in raw soybeans inoculated with the "Itobiki" strain of *B. natto* while the NRRL B-3383 strain of *B. natto* increased lipid content by 1.1-fold (Wei and Chang, 2004). Thus, different *B. natto* strains have different capabilities to synthesize lipid or utilize carbohydrates during fermentation (Wei and Chang, 2004). Another notable compositional change in natto is the significant increase in vitamin K content after fermentation. The extraordinary increase in vitamin K in *natto* has been attributed to vitamin K2 (menaquinone-7 or MK-7) synthesis by *B. subtilis natto* (Kouris-Blazos and Belski, 2016). Epidemiological studies have also shown that increased consumption of Japanese *natto* is positively correlated with bone density among Japanese females as a result of increases in serum vitamin K and ϒ-carboxylated osteocalcin, both of which facilitate bone mineralization (Tsukamoto et al., 2000; Katsuyama et al., 2002). For water-soluble vitamins, fermentation was reported to increase thiamine and riboflavin contents by 3-folds and a 5-fold increase in vitamin B12 content compared to the raw substrate (Reddy et al., 1983).

Kinema (**Figure 3B**), a fermented-soy condiment, is a traditional delicacy produced in Nepal and parts of India. *Kinema* not only possesses exceptional flavor but has a significant dietary importance as a relatively cheap substitute for meat (Sarkar et al., 1994). Like other soy-based fermented products, *kinema* is a rich source of protein (43.4–48.7%), fat (16.1–22.7%), carbohydrates (27.4–29.6%), and minerals (**Table 1**). The nutrient composition of *kinema* has previously been reported (Sarkar and Tamang, 1995; Sarkar et al., 1997b, 1998). Total protein content of *kinema* increases by about 1% while free amino acid content increases by 60-fold compared to raw soybeans. However, for its dietary role as meat substitute, tryptophan, cysteine, and methionine are the main limiting amino acids in *kinema*, although protein quality has been reported to be comparable to animal source protein (Sarkar et al., 1994, 1997b). B-vitamins in *kinema* varies from the raw soybean substrate with general increases in levels of riboflavin and niacin, but a decrease in thiamine (Sarkar et al., 1998). The minerals content of *kinema* was also reported to be lower than raw soybean. The decline in the mineral level in *kinema* has been attributed to the preparation process where soybeans are soaked, cooked, and the water discarded (Sarkar et al., 1998).

Doenjang (**Figure 3C**) is an indigenous alkaline fermented soybean paste which serves as an important protein source and seasoning agent in the traditional diets of the people of Korea. *Doenjang* is considered a nutritious food that provides essential amino acids, fatty acids, minerals, and vitamins, associated with various nutritional benefits. Proximate composition of *doenjang* include 54.7% water, 13.8% crude protein, 8.0% crude lipid, 14.4% (Park and Jung, 2005). Amino acids composition of *doenjang* include glutamic acid, leucine, alanine, histidine, lysine, proline, and valine (Park and Jung, 2005). Fermentation of *doenjang* for 80 days results in relative increases in methionine and threonine levels compared to raw soybeans. However, these amino acids are still limiting in *doenjang* and therefore other dietary strategies such as complementation would ensure adequate intake of essential amino acids (Namgung et al., 2010). Like *doenjang*, *chongkukjang* is another traditional Korean soy-based fermented food, similar to Japanese *natto*, but different in usage (Chukeatirote, 2015). *Chongkukjang*, commonly consumed for its perceived health-promoting properties, is also regarded as a rich source of proteins, lipids, amino acids, vitamins, and minerals (Ali et al., 2018). Fermentation of soybean into *chongkukjang* with higher concentrations (5–7%) of *B. subtilis* enhances the minerals content of the product (Ali et al., 2018). The significant improvement of minerals content has been attributed to microbial involvement and interaction with metabolites breakdown (Ali et al., 2018). Fermentation is also reported to degrade antinutritional factors during c*hongkukjang* processing, invariably improving the bioavailability of minerals (Ali et al., 2018). The microorganisms' strains in the fermentation process significantly influence the product's value. The total mineral contents in *chongkukjang* fermented with *Bacillus amyloliquefaciens* RWL-1 increased by about 33% compared with the quantity obtained from the conventional *B. subtilis* (Shahzad et al., 2020).

Douchi (**Figure 3D**), a nutrient-rich fermented soy-based food product, is widely used seasoning in China and other Asian countries to enhance appetite (Li and Ma, 2014). During *douchi* production, a series of complex biochemical reactions enhance chemical and nutritional components in the raw soybeans. During fermentation, proteins are converted to peptides and amino acids, lipid to fatty acids, starch to reducing-sugars and ethanol, and various aroma components by salt-tolerant microorganisms (Li and Ma, 2014). The crude protein and fat content of *douchi* ranges from 35.9–40.4 to 19.9–23.9%, respectively (**Table 1**). The crude protein content of pre-fermented *douchi* slightly increased and then decreased by 1.2-fold after four (4) weeks of ripening (Wang et al., 2016). The fermentation process is also reported to increase the product's mineral content and bio-accessibility (Liu et al., 2020).

Meitauza is produced from *okara* (a by-product from the production of soybean foods such as soymilk and *tofu*) in China. Crude protein content of *meitauza* declines by almost 6% due to the interaction between microbes and the fermenting media. However, total free amino acids significantly increased during the fermentation process (Xu et al., 2012). Strong-tasting amino acids such as glutamic acid and glycine increase by over 10-folds; and aspartic acid, alanine and arginine increased several-fold. Similarly, amino acid with sweet taste: leucine, valine, serine, and methionine significantly increase during fermentation, improving the taste and overall nutritional value of the fermented product. Although *okara* contains high moisture content (>80%), the water is linked to dietary fiber, resulting

TABLE 2 | Summarized nutritional information previously reported for some AFFs.

Plant-based AFF	Proximate (unit/100 g)							Minerals (mg/100 g)						
	Moisture (g)	Crude Protein (g)	Crude Fat (g)	Total Ash (g)	CHO (g)	Fiber (g)	Energy (kcal)	Fe	K	Ca	Mg	P	Zn	Cu
Legume; soybean products														
Natto	60.8–64	40.7–49.6	18.0–24.7	4.7–5.6	23.3–29.9	3.49–3.55	494	8.1–12.4	1,600	220–416	250	470	4.70	1.51
Douchi	NA	35.9–40.4	19.9–23.9			NA	NA	NA	NA	NA	NA	NA	NA	NA
Kinema	57.3–64.8	43.4–48.7	16.1–22.7	5.6–7.4	27.4–29.6	NA	430–501.7	17.7	1,768	432	252	12.6	4.52	1.71
Doenjang	54.7	13.8–23.4	8.0	21	45.4	3.1	NA	NA	NA	NA	NA	NA	NA	NA
Chongkukjang	57.7–62.8	14.8–20.9	5.4–8.5	1.4–2.3	8.6–16.3	NA	NA	3.8–31	602–1,099.3	96–166.7	89.2–101.9	177	2.9–3.7	1.01–1.4
Thuo nao	56.4–64.9	38.9–42.8	3.2–25.2	4.7–7.9	33.6–40.3	NA	NA	11.8	1,478	386	240	778	6.13	1.48
Meitauza	74.5	30.6–39.4	8.5–11.6	4.07–5.06	15.9–32.4	NA	NA	NA	NA	NA	NA	NA	NA	NA
Soy-dawadawa	11.4–25	43.2–47.4	19.9–26.7	3.5–5.0	16.2	4.5	NA	NA	1,460	2,400	192	388	NA	NA
Legume; non-soybean products														
dawadawa	10.2	49.7	26.9	4.32	7.43	6.5	NA	1.67–2.0	1,322	637	136	375	3.17–3.76	112–119.8
Ugba		17.13–35.4	36.3–61.4	1.11–2.9	17.48	2.9–5.6	NA	4.25	11.04	20.9	33.5	29.1	0.9	NA
Kawal	NA	24.32–30.2	2.95–4.12	18.16–20.04	16.86–25.89	19.3–21.8	221.59–232.88	2.97–4.37	1,026–1,543.6	2,114.7–2,571	212.8–241.4	98.6–115	0.45–0.53	0.72–1.54
Okpehe	*65–65.3*	38.7–40.06	11.96–12.3	2.2–2.3	0.15–0.17	0.38–0.51	NA	58.8	303.8	68	63	540	10.1	1.8
Oso	40.3	16.9	16.9	1.03	10.02	6.45	NA	1.8	NA	129	NA	720	6.38	1.4
Non-legume products														
Ogiri	27–31	21.4–22.9	20.8–22.3	3.07–3.47	15.2–21.4	5.2–6.4	NA	36–75		10	686–716		38–69	19–21
Furundu	28.7–39	21.8–24.6	5.5–7.7	16.9–22.8	14.4–14.7	NA	19,400–21,210	1,290–1,300	68–74	144–122	552–599	8,560–10,400	6,933–7,830	NA
Bikalga	8.2.4	26.47	23.19	9.03	13.7	NA	NA	1.1–17.5	0.5–28	0.34–28.6	NA	0.15–1.7	0.09–9.1	0.2–1.9
Mbuja		3.9–5.95	12.9–31.9	1.8–2.3		13.2–32.4	NA	19.8	NA	128.3	418.6	NA	6.4	0.3
Maari	10.3–13.4	13.4–14.7	15.1–18.1	0.68–0.88	4.65–5.11	NA	NA	0.55	0.77	0.57	NA	303	1.8	0.02
Owoh	46.6	13.6–28.6	15.3–42.8	1.25–6.1	13.7–15.7	NA	NA	24.7	0.07	0.15	0.08	0.03	12.4	3.1

NA, Not available. All data on dry matter basis except for moisture.

in the pasty texture of the by-product (Redondo-Cuenca et al., 2008). The fiber, largely insoluble cellulose and hemicellulose, form a more significant part of the dry matter content (40–60%). Fermentation can increase the soluble fiber level in *okara*, improving its nutritional quality and processibility (Sharma et al., 2020). It also induces a significant decrease in lipid and lignin contents in *okara*. These compositional changes have led to a pleasant and delicate taste, as well as a smooth and rubbery texture (Colletti et al., 2020).

Dawadawa (**Figure 3E**) is the most important protein-rich food condiment in West and Central African, primarily used as a meat substitute or to enhance the organoleptic qualities of traditional staple foods. *Dawadawa* is known by different local names depending on the country of production; *dawadawa* in Ghana, *iru* (Nigeria), *nététu* (Senegal), *kinda* (Sierra Leone), *afitin, iru, or sonru* (Benin) and *soumbala* (Burkina Faso). Varying nutritional composition have been reported for *dawadawa* because a range of raw materials including locust bean, bambara groundnuts [*Vigna subterranean* (L.) Verdc.], and soybean serve as substrates for the fermentation (Achi, 2005). In general, locust bean is inedible and could be toxic to humans (Wang and Fung, 1996). However, a significant reduction in the anti-nutrient content and enhanced amino acid profile has been reported for alkaline fermented locust bean (Ijarotimi and Keshinro, 2012). Generally, *dawadawa* produced from African locust beans contain about 49.7% protein, 26.9% lipids, 4.3% total ash, and 7.4% carbohydrates (Appiah et al., 2012). Alkaline fermentation of African locust bean resulted in an increase in total protein content and an improvement in the amino acid profile (Urua et al., 2013). This increase in free amino acids levels due to the proteolytic activities by the fermentative microorganisms have been reported for *dawadawa* (Odunfa, 1981; Akabanda et al., 2018). Additionally, fermentation of locust bean results in a 6-fold increase in thiamine and 3-fold increase in riboflavin contents, but a reduction (30%) in niacin content. Similar reduction in niacin content was reported for *ugba*, fermented condiment from African oil bean seeds, corresponding to progressive reduction in cyanide, phytate, tannin and oxalate contents (Ogueke et al., 2013). Sulfur-containing amino acids are generally limiting in locust bean *dawadawa* (Campbell-Platt, 1980) and *ogiri* produced by alkaline fermentation of melon seeds, but these could be complemented through the consuming the AFFs with cereal-based staples (Wang and Fung, 1996). For *soy-dawadawa*, fermentation protein, carbohydrates and fat contents are reported to be 43.2–47.4, 16.2, and 19.9–26.7%, respectively (**Table 2**). The major biological changes occurring during *soy-dawadawa* processing include hydrolyses of protein, fat, and carbohydrate, with the fermentation leading to increased contents of protein and amino acids such as lysine, arginine, proline, phenylalanine, isoleucine, and leucine (Dakwa et al., 2005; Terlabie et al., 2006).

In Congo and parts of central Africa, cassava (*Manihot esculenta* Crantz) leaves are fermented to produce *ntoba mbodi* (Louembe et al., 2003). *Ntoba mbodi* is relatively rich in protein although a slight reduction in free nitrogen occurs during fermentation, probably due to liberation of hydrogen cyanide. Extensive cellulase activity, through fermentation, further enhances the bioavailability of carbohydrates and increases magnesium, calcium, and potassium contents in *notba nbodi* compared to raw cassava leaves. However, methionine and phenylalanine are the limiting amino acids in *ntoba nbodi* (Mokemiabeka et al., 2011). Another product similar to *ntoba nbodi* is *kawal* produced by the fermentation of sickle pod [*Senna obttusifolia* (L.) H.S/Irwin & Barneby] leaves in Chad and Sudan where it serves as meat substitute and flavoring agent soups and stews (Dirar, 1984; Harper and Collins, 1992). While Dirar (1984) reported a decrease in crude protein content of after fermentation, Harper and Collins (1992) reported increased crude protein content of *kawal*. Although about 50% protein loss during the fermentation of *kawal* has been observed, the loss is overshadowed by the substantial increase in digestibility and palatability of the fermented product. Limiting amino acids in *kawal* include cysteine, histidine, and threonine. However, *kawal* is consumed with cereals foods which may provide complementary proteins (Mbaiguinam et al., 2005).

HEALTH PROMOTING EFFECTS OF AFFs

Production of Vitamins

All vitamins are essential for human growth—meaning human cannot synthesize adequate quantities of vitamins *de novo*, if at all. Therefore, human diet must contain adequate quantities of these vitamins in order to maintain normal growth and bodily functions. These vitamins act as co-factors or pre-cursors to important metabolic processes and enzymes in living organisms. Fermentation is touted as a natural process for the *in-situ* biosynthesis of vitamins in food materials (Odunfa, 1986). As shown in **Table 3,** examples of vitamins whose levels have been significantly increased after fermentation are Vitamin K and the B-vitamins (e.g., thiamine (B_1), riboflavin (B2), niacin (B3), pantothenic acid (B5), pyridoxal (B6), biotin (B7), folate (B9), and cobalamins (B12).

The biosynthetic pathways for the production of vitamins B2 (Burgess et al., 2009), B12 (Burgess et al., 2009), B9 (Rossi et al., 2011), and other B-type vitamins have been widely reported in lactic acid bacteria (LeBlanc et al., 2011). Among alkaline-fermenting bacterial strains, *B. subtilis* (Bacher et al., 1980; Bretzel et al., 1999; Li et al., 2013; Man et al., 2014), *B. tequilensis* (Abdulla et al., 2016), *B. abortus* (García-Angulo, 2017), *B. amyloliquefaciens* (Vitreschak et al., 2002), and *B. halodurans* (Averianova et al., 2020) are the most studied species.

Most food-grade microorganisms, including those found in alkaline fermented foods have the genetic wherewithal to synthesize vitamins during growth on organic materials. The class of genes needed for the biosynthetic of these vitamins differ for each vitamin but can be intricately linked, as is the case for vitamin B2, B9, and B12 (Gu and Li, 2016). In *B. subtilis*, the production of Vitamin B2 begins with the expression of *ribA* gene which encodes for the bifunctional enzyme guanosine $5^{\prime}$-triphosphate (GTP) cyclohydrolase II/3,4-dihydroxy-2-butanone 4-phosphate synthase responsible for the conversion of GTP to 5-amino-6-ribityl-amino-2,4(1H,3H) pyrimidinedione (ArP), and ribulose 5-phosphate (Ribu5P) to 3,4-dihydroxy-2-butanone-4-phosphate (DHBP). ArP and

TABLE 3 | Improvement in vitamin availability of some AFFs.

Product name	Vitamin type	References
Legume; soybean products		
Chongkukjang (also written as *Chungkukjang*)	B_{12}	Kwak et al., 2010
Doenjang	B_{12}, E	Kwak et al., 2010; Shin and Jeong, 2015
Furu	B_{12}	Li et al., 2004
Gochujang/Kochujang	C	Shin et al., 2012
Hawaijar	B_2, K	Khan et al., 2016
Kanjang	B_{12}	Lee et al., 1959
Kinema	B complex	Tamang, 2012
Tempe	B2, B3, B6, B_9, B_{12}, E,	Watanabe et al., 2014; Mani and Ming, 2017
Thuo nao	B_{12}	Yongsmith et al., 2016
Tungrymbai	K	Dihingia et al., 2018
Meju	D	Ahn, 2018
Miso	K	Tarvainen et al., 2019
Natto	K	Tarvainen et al., 2019
Soy sauce	K	Tarvainen et al., 2019
Legume; non-soybean products		
Dawadawa	B1, B2, B3, C, B6, B9, B12, D, E	Oguntoyinbo et al., 2016; Termote et al., 2022

DHBP are the two substrates of riboflavin (Vitamin B2) (Averianova et al., 2020). Plant-based food products whose riboflavin levels have been significantly improved *via* alkaline fermentation include *dawadawa* (Oguntoyinbo et al., 2016), *kinema* (Sarkar et al., 1998), and *tempe* (Mani and Ming, 2017).

The production of folate also begins with GTP which acts as a precursor for 6-hydroxymethyl-7,8-dihydropterin pyrophosphate (DHPPP) through a series of four enzymatic conversion steps. Another important substrate for folate production is para-aminobenzoic acid (pABA) which is produced from erythrose 4-phosphate and phosphoenolpyruvate through the shikimate pathway (Bermingham and Derrick, 2002). The coupling together of DHPP and pABA, and subsequent glutamylation of the final product gives polyglutamate forms of dihydrofolate (DHF), and tetrahydrofolate (THF) (Rossi et al., 2011).

Cobalamin (Vitamin B12) has an intricate and complex structure. It is no wonder that as many as 30 genes are required for its biosynthesis (Gu and Li, 2016). One of the few *Bacillus* species known to synthesis Vitamin B12 *de novo* is *B. megaterium* where the synthesis occurs through an anaerobic route (Fang et al., 2017). *B. megaterium* is considered a producer of Vitamin 12 at the industrial scale (Vary, 1994; Mohammed et al., 2014). In this species, uroporphyrinogen III is first converted to precorrin-2 and then subsequently to cobyric acid. The transformation of precorrin-2 to cobyric acid occurs through a series of reactions involving eight methylations, six amidations, insertions of cobalt, and decarboxylation and contraction of the porphyrin ring (Moore and Warren, 2012). Cobyric acid is converted to cobinamide, and then to cobalamin.

Kwak et al. (2008) reported the Vitamin B12 contents of traditionally fermented *Doenjang* and *Chungkookjang*, two Korean soybean-based fermented foods, and found levels of 1.85 mg/100 g and 0.69 mg/100 g, respectively. These levels were significantly higher than those found in factory-made versions of the products which had 0.04–0.86 mg/100 g and 0.06–0.15 mg/100 g, respectively. The high levels of Vitamin B12 in the traditional fermentation process could be due to the fact that the traditional process to prepare *Doenjang* and *Chungkookjang* is relatively long (∼ about 10 months) and uses "wild-type" multiple microorganisms found in nature (Kwak et al., 2010).

Vitamin B12 production to levels of about 91.43 mg/100 dw in in fermented soybean, *Thua nao* (**Figure 3F**) using mixed culture fermentation using mixed cultures of *B. amyloliquefaciens*. and *Klebsiella* spp. have been reported (Yongsmith et al., 2016). The levels of Vitamin B12 in tempeh (i.e., 0.7–8.0 mg/100 g), (Watanabe et al., 2014). The levels of Vitamin B12 in *natto* has been reported to be over five times that in cooked soybeans (Wang and Fung, 1996).

The fact that the aforementioned vitamins are abundant in alkaline fermented plant-based foods suggest that fermentation can be considered as suitable chemical-free production route for these vitamins, for use in supplements and food fortification programs (Gu and Li, 2016). Further, in some cases (such as in riboflavin synthesis) production of these vitamins *via* fermentation leads to products with higher chemical purity, compared with chemically synthesized alternatives (Bretzel et al., 1999).

Improved Digestibility

In general, plant-based foods are comparatively less digestible than animal-based foods, when subjected to the human digestive system. The low digestibility of plant materials is due to factors such as the presence of cellulose cell wall that decrease access by enzymes to target molecules (Holland et al., 2020), the inability of human gastro intestinal enzymes to digest cellulose (Cummings, 1984), restrictive structural features of target molecules (e.g., hydrophobicity and folding patterns of plant proteins), presence of "antinutritive" compounds or secondary metabolites that inhibit human gastric enzyme activities (Sarwar Gilani et al., 2012), complexation of target molecules with other compound (e.g., starch-lipid conjugates) (Qin et al., 2019), among others. All of these aforementioned phenomena decrease the digestion, bioaccessibility, and bioavailability of nutrients in plant-based foods. The ability of alkaline fermentation to improve the digestibility of plant foods therefore strongly depends largely on microbial metabolic processes that affects one or more of the above-mentioned factors. The description (with examples) of two pathways through which fermentation increases the digestibility of certain alkaline-fermented foods is given below.

Partial Hydrolysis and Release of Hydrolytic Products and Their Metabolites

The action of alkaline fermentation leads to the generation of a host of factors that directly or indirectly causes partial hydrolysis or softening of plant matrix. For example, microbial enzymes produced *in situ* during fermentation can utilize biomolecules in plant matrices as substrates, leading to the generation of partially-hydrolysed plant microstructures and release of hydrolysis products. Case in point, proteolysis is considered the most important metabolic activity in alkaline fermentation (Parkouda et al., 2009), and increased protease activity during alkaline fermentation is well-reported (Ouoba et al., 2003; Owusu-Kwarteng et al., 2020). Proteolysis is mostly caused by *Bacillus* spp. (Ouoba et al., 2003), and this biochemical process leading to the formation of peptides and free amino acids that improve the nutritional qualities of the fermented product. The levels of essential amino acids such as methionine, cysteine, leucine, tyrosine, phenylalanine, and lysine have been reported to increase after alkaline fermentation (Ouoba et al., 2003; Owusu-Kwarteng et al., 2020). The released free amino acids are further metabolized by the microorganisms to ammonia, giving rise to the characteristic pungent "ammonia-like" odors of some traditional fermented foods such as *dawadawa* (Parkouda et al., 2009). High pH is known to degrade cellulose and lignocellulose (Glaus and Van Loon, 2008). Therefore, the production of ammonia and accompanying high pH during alkaline fermentation can be expected to indirectly "soften" plant compounds, making them more susceptible to the actions of subsequent food processing and gastrointestinal enzymes.

Reduction in Levels of Antinutritional Factors and Flatus-Forming Oligosaccharides

Plant materials are rich in antinutritional factors such as lectins, tannins, saponins, protease inhibitors, oxalic acid, cyanogenic glycosides, and phytic acid. These antinutritional factors can reduce the bioavailability of key nutrients (such as vitamins and minerals), or interfere with the activities of gastro-intestinal digestion. Some antinutritional compounds (e.g., hydrocyanic acid released from cyanogenic glycosides) can be toxic to humans.

The seeds of African locust bean (*Parkia biglobosa*), used in the preparation of *dawadawa* contains antinutrients such as nitrates, tannins, cyanide, phytates, and oxalates (Termote et al., 2022). Urua et al. (2013), in their work on the effect of processing on three accessions of African locust bean reported that fermentation reduced the levels of phytic acid and oxalates respectively by up to 44.4 and 50.9% each; whereas boiling reduced the levels of these antinutrient by up to 33.3 and 4.4%, respectively. The oxalate contents in two of the accessions actually increased by 140.8 and 78.1%, respectively (Urua et al., 2013). In another study, trypsin inhibitor activity, tannins, and phytic acids in African locust bean seed were reduced significantly by 89.0, 59.8, and 62.5%, respectively after 72 h of alkaline fermentation (Esenwah and Ikenebomeh, 2008). In other reports, alkaline fermentation of soy beans into *kinema* has been shown to reduce the levels of tannins, phytic acids, trypsin inhibitor activity, and haemagglutinating activity by 100, 61, 71, and 100%, respectively (Sharma et al., 2015). Kobawila et al. (2005) have demonstrated that the cyanogenic glycoside content reduced significantly by 70–75% during alkaline fermentation of cassava leaves (Kobawila et al., 2005). These examples demonstrate that alkaline fermentation degrades antinutritional compounds, thereby reducing or eliminating them from the fermented food.

Improved Health Benefits *via* the Actions of Probiotics and Post-biotics

Many of the *Bacillus* strains predominant in alkaline fermented foods are also used commercially as probiotics. Some of these strains *include B. cereus, B. clausii, B. coagulans, B. licheniformis, B. polyfermenticus, B. pumilus,* and *B. subtilis*—all of which exhibit probiotic activities in both spores and vegetative forms (Lee et al., 2019). Compared to probiotic lactic acid bacteria, Bacillus probiotic strains have better survival rates and stability to processing conditions such heat, cold, moisture, dehydration, as well as gastric conditions (Lee et al., 2019). This feature of *Bacillus* probiotics is largely due to their ability to form spores (Nicholson et al., 2000). In fact, the ability of *Bacillus* spores to germinate and grow in the gastro-intestinal tract has been reported (Hoa et al., 2000). This means that fermented pant-based foods could be used as carriers for the delivery of *Bacillus* probiotics into the mammalian digestive systems.

The influence of probiotics on human gut microbiome is well-reported (Thursby and Juge, 2017; Kawai et al., 2018), but the focus of has mostly been on lactic acid bacteria probiotics. Whereas, the impact of individual *Bacillus* strains on gut microbiome of some animal model (e.g., chicken and pigs) have been studied (Poulsen et al., 2018; Jacquier et al., 2019), little is known on how specific *Bacillus* strains influence the human gut microbiome. It is however known that, as probiotics, *Bacillus* strains stimulate antimicrobial, anticancer, antihypertensive, antioxidant, fibrinolytic, and immunomodulating activities *in vitro* and *in vivo* (Lee et al., 2019). These biological properties can be stimulated by the metabolic process of probiotics and post-biotics in alkaline fermenting foods.

Post-biotics are the bioactive soluble by-products released following either through the metabolic processes of probiotics or through lysis of probiotics (Wegh et al., 2019). A technical definition of post-biotics, as proposed by The International Scientific Association of Probiotics and Pre-biotics (ISAPP) is "preparation of inanimate microorganisms and/or their components that confers a health benefit on the host" (Salminen et al., 2021).

There is a growing number of studies reporting the health properties of post-biotics (Wegh et al., 2019; Zółkiewicz et al., 2020; Salminen et al., 2021) but these studies do not discriminate the source of these post-biotics, i.e., whether

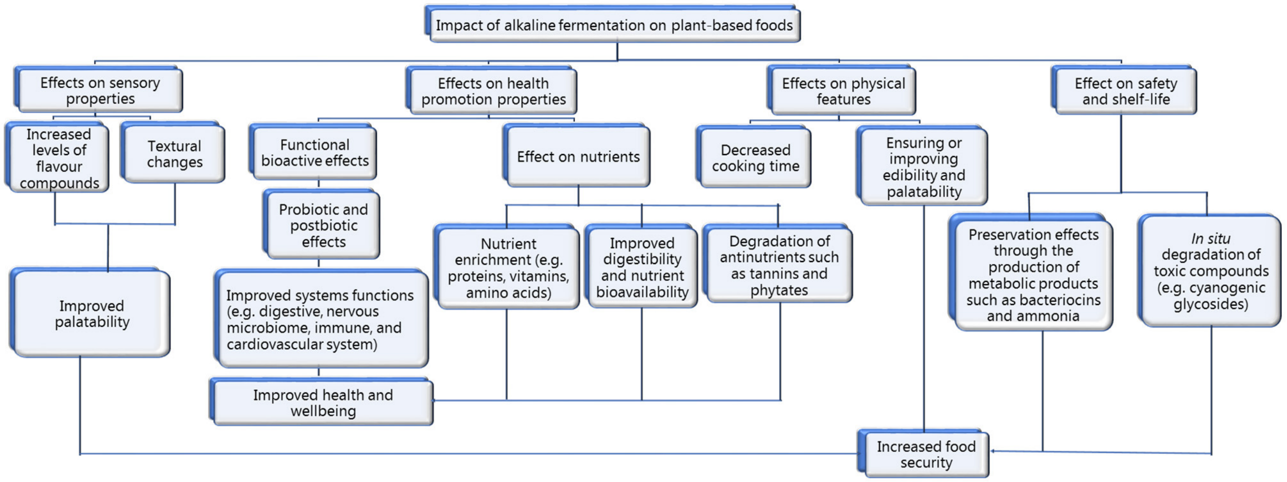

FIGURE 4 | Impact of alkaline fermentation on plant-based foods.

from acid or alkaline fermentation. However, examples of post-biotics that can be expected to be produced following alkaline fermentation of plant-based foods are soluble proteins, protein hydrolysates, bacteriocins, free amino acids, vitamins, soluble dietary fiber, exopolysaccharides, non-viable cells, and cell fragments. As presented earlier (see Sections Nutritional and Dietary Value of Plant-Based AFFs), alkaline fermentation leads to the production of several probiotics-derived biomolecules, many of which can be expected to have bioactive properties. Some of the mechanisms through which post-biotics mediate health in hosts includes mediating growth and metabolic activities of gut microbiota, modulating systemic metabolism, mediating signaling in nervous system, enhancing epithelial barrier function, modulating immune responses, triggering bioactive properties such as anti-adhesion, anti-biofilm, antidiabetic, antiviral, immunomodulatory, antihypertensive, hypocholesterolemic, and antioxidant effects (Tangyu et al., 2019; Wegh et al., 2019; Nataraj et al., 2020; Zółkiewicz et al., 2020; Salminen et al., 2021). A schematic of the nutrition and health impact of alkaline fermentation on plant-based foods is shown in **Figure 4**.

CONCLUSION AND FUTURE OUTLOOK

As shown in the preceding discussion, alkaline fermentation of plant-based foods offers several sensorial, nutritional, and health benefits. For example, guided selection of starter cultures and probiotic strains could be used to stimulate the *in situ* biofortification of plant-based foods through alkaline fermentation as a strategy to prevent deficiencies in nutrients such as vitamins, minerals, and proteins. However, as demonstrated in this review, the scientific underpinnings of the microbial metabolic factors and health-promoting effects of AFFs are not as well-studied as other fermented foods produced *via* lactic acid fermentation. For example, a careful search of the literature shows that only a few *Bacillus* species have been studied for their vitamin production potential, with *B. subtilis* being the most studied. Even then, most of the fundamental scientific studies on vitamin-producing alkaline fermenters were performed at laboratory scale using genetically modified strains, and in chemically defined media. The production of vitamins by alkaline fermenters *in situ* in plant-based foods needs more investigation.

Moreover, perspectives for improving the traditional production processes of AFFs to ensure consistency in safety and quality should be researched. Research is needed to unravel the genome sequences of microorganisms in AFFs. This will help with proper identification and taxonomic classification of species responsible for the generation of desired properties. Genomic sequences of microbiota in AFFs will also allow the selection of genes that can be targeted and altered by metabolic engineering strategies, to improve desired traits such as the production of post-biotics (e.g., enzymes, vitamins, bacteriocins, and exopolysaccharides), or to isolate and exclude genes responsible for the production of biogenic amines and antibiotic resistance genes. Another important area that needs attention is the generation of clinical evidence on how the composite microbial species in AFFs alter human gut microbiome. For reasons such as relatively low cost of production and the aforementioned nutritional and health promoting benefits, AFFs are expected to play a huge role in meeting the food, dietary, and health requirements of consumers, going forward.

AUTHOR CONTRIBUTIONS

JO-K designed the manuscript. JO-K and DA critically revised and corrected the manuscript. JO-K, DA, FA, RA, and FKA wrote the manuscript. All authors contributed to the article and approved the submitted version.

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