



Review

Changes Occurring in Spontaneous Maize Fermentation: An Overview

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Abstract: Maize and its derived fermented products, as with other cereals, are fundamental for human nutrition in many countries of the world. Mixed cultures, principally constituted by lactic acid bacteria (LAB) and yeasts, are responsible for maize fermentation, thus increasing its nutritional value and extending the products' shelf-life. Other microorganisms involved, such as molds, acetic acid bacteria, and *Bacillus* spp. can contribute to the final product characteristics. This review gives an overview of the impact of the activities of this complex microbiota on maize product development and attributes. In particular, starting from amylolytic activity, which is able to increase sugar availability and influence the microbial succession and production of exopolysaccharides, vitamins, and antimicrobial compounds, which improve the nutritional value. Further activities are also considered with positive effects on the safety profile, such as phytates detoxification and mycotoxins reduction.

Keywords: fermentation; maize; fermented products; microbiota; starch degradation; phytates detoxification; mycotoxins reduction; antimicrobial activity

1. Introduction

Maize or corn (*Zea mays*) is a graminaceous annual plant whose origin is linked to America. It was introduced into Europe in the sixteenth century, then spread outside the continent, across Africa and Far East Asia, and due to its exceptional geographic adaptability, nowadays, it is considered as one of the most important cereals in the world. Maize is a good source of metabolizable energy, and in spite of the poor protein content, it is also considered as a vital food grain in many countries, and in particular, in Africa, Asia, Central, and Southern America.

In recent years, the number of reports describing the fermentation process around the world, as well as the microorganisms involved in maize-fermented products, particularly from Africa and Latin America, has significantly increased. Table 1 reports the most common maize-based fermented food products and their principal technological characteristics, such as fermentation time and temperature, pH, and ethanol content.

Fermentation is recognized as a natural way to preserve and safeguard foods and beverages, enhancing the nutritional value, improving the digestibility, destroying undesirable components, and inhibiting undesirable microorganisms [66]. However, in artisanal fermented products, biological risks such as pathogenic microorganisms, as well as chemical contaminants and toxic molecules of microbial origin, including mycotoxins, biogenic amines, and cyanogenic glycosides can be found [67]. For this reason, a deep understanding of the role of the different microbial groups developing in spontaneously fermented products is of crucial importance to optimize the final quality and to improve the food safety of these products.

Table 1. Maize-based fermented food products and their technological characteristics.

Name of Product	Country	Food Category	Fermentation Time–Temperature	pH	Ethanol Content (v/v %)	References
Akamu	Nigeria	Porridge	72 h, 28–30 °C	3.2–3.9	-	[1–3]
Atole agrio	Mexico	Beverage	6–12 h, 34 °C	3.9	-	[4,5]
Busaa	Kenya, Nigeria, Ghana	Beverage	5–7 d + 2–3 d, room T	3.5–4.0	3.5–4.8	[6–8]
Champús	Colombia, Ecuador, Perú	Beverage	24–48 h, 12–15 °C	3.5–4.0	2.5–4.2	[9,10]
Chicha	Argentine	Beverage	3–7 d + 2 d, room T	3.6–3.8	2.0–12.0	[11,12]
Chicha	Colombia	Beverage	2–6 d, 18–32 °C	3.5–4.6	2.0–12.0	[10]
Doklu	Côte d’Ivoire	Dough	2–4 d, room T	2.2–3.8	-	[13–15]
Gowé	Benin	Dough	16 h, room T	3.6–4.1	-	[16–18]
Ilambazi lokubilisa	Zimbabwe	Porridge	2–4 d, room T	n.a.	-	[19]
Ikii	Kenya	Porridge	n.a.	3.9	-	[20,21]
Kachasu	Zimbabwe	Beverage	4–7 d, room T	n.a.	9.0–41.0	[7,19,22]
Kenkey	Ghana	Dough	2–4 d, room T	3.7	-	[23–26]
Koko	Ghana	Porridge	2 d, room T	n.a.	-	[7,27]
Kokoro	Nigeria	Snack	24 h, 27–31 °C	6.2	-	[28,29]
Kutukutu	Cameroon	Dough	120 h, 25–30 °C	2.7–3.1	-	[30]
Mahewu/Amahewu	South Africa, Arabian gulf countries	Beverage	24–72 h, room T	3.5–3.6	-	[31–35]
Masa agria	Colombia	Dough	3–5 d, 35–40 °C	3.1–4.4	-	[10,36,37]
Massa	Nigeria	Snack	12–24 h, room T	n.a.	-	[38]
Mawè	Benin, Togo	Dough	72 h, 28–32 °C	3.8–4.2	-	[16,39–41]
Munkoyo	Katanga, Zambia, Southern Democratic Republic of Congo	Beverage	24–48 h, 25–30 °C	3.5–4.0	0.0–2.7	[42–44]
Mutwiwa	Zimbabwe	Porridge	room T	n.a.	-	[19]
Ogi	Nigeria	Porridge	48–72 h + 24–48 h, 28–30 °C	3.8–4.1	-	[16,45–49]
Pito	Nigeria	Beverage	12 h + 12 h, room T	4.9	3.0–4.0	[50,51]
Poto poto	Congo	Dough	55 h + 10–11 h, room T	3.7–3.8	-	[52–54]
Pozol	Mexico	Dough	2–7 d, room T	4.2–4.6	-	[55–60]
Sekete	Nigeria	Beverage	2–3 d, room T	2.8–4.3	0.9–4.0	[61,62]
Tesguino	Mexico	Beverage	2–3 d, room T	n.a.	3.7	[63]
Togwa	Tanzania	Beverage	12–24 h, room T	3.1–3.3	-	[64,65]

n.a., not available.

In a fermented product, the metabolic activity reflects the metabolic capabilities of the different species or microbial groups that, together with the technological characteristics of the process, influence the sensorial properties of spontaneously fermented products [9]. In fact, microbial interactions in mixed cultures, taking place in fermented products, occur via multiple mechanisms, and the effects of such interactions on the fitness of the strains involved may be either positive, neutral, or negative [68]. Taking into account that any spatial or temporal change in the community composition can consequently modify this complex ecosystem, then the role of the different species on flavor, rheology, and shelf-life, as well as on the functional/nutritional characteristics, has been a matter of study. In the light of these considerations, in this review, we will focus on important activities that occur during maize fermentation, with particular emphasis on those determining the microbial succession and the development of fermentation, such as the increased sugar availability by the degradation of starch, and the production of exopolysaccharides, vitamins, and antimicrobial compounds. In addition, we will also consider the microbial action that also provides detoxification of phytates and reduction of mycotoxins.

2. Maize Fermentation

Around the world, maize grains are processed and fermented following different traditions to obtain a great diversity of products. In general, fermented maize production initially involves the cleaning of the grains, which are then successively soaked in water until soft and ground when wet, followed by fermentation. Domínguez-Ramírez et al. [69] classify the methods used to prepare fermented maize products into 4 categories according to the methods in which foods are made with: 1) dried kernel, 2) complete maize ears soaked, 3) maize flour and 4) mashed tender maize. Moreover, on the basis of the texture, fermented maize products can be classified into liquid (gruel and porridges), such as *ogi*, *dalaki*; *chicha*, *champus*, and *boza*; solid (dough and dumplings), such as *masa agria*, *pozol*, *kenkey*, *akidi*, and *komé*; and dry (baked, fried, and steam-cooked granulated products), such as *arraw*, *dégué*, *masa*, and *wômi* [70].

Before maize fermentation, some traditions provided the use of a pretreatment such as nixtamalization, a process where the maize grains are soaked with an alkali (generally lime), then cooked, dried, and ground to obtain the flour; grain germination, and chewing. These actions lead to physical and chemical changes in the grains, thereby acting as selective agents for the microbiota that guides the fermentation process in this modified substrate. Microorganisms utilize a large number of nutrients present in the grains, and their metabolism is a major driving force in the regulation of microbial diversity and activity on the fermented maize. The fermentation processes modify the grains through various steps, in which endogenous enzymes (amylases, proteases, phytases, etc.) and microbial enzymes (usually from lactic acid bacteria and yeasts) are involved [71]. The microbial activity in maize dough or slurry is a well-defined temporal succession of naturally occurring microorganisms that are usually found in association with each type of fermentation.

In uninoculated fermented products, microorganisms principally derived from the raw materials can also be affected by the phytochemical treatments of maize or by the environmental features, such as temperature, rainfall, or insect attacks during cultivation [36]. In addition, the microbial diversity of this kind of fermented product can generally be contributed to by the water employed during the production, as well as the tools (e.g., spoons, pots, etc.), the contact with wooden tables, or the exposition to the air, and particularly the step of grinding and soaking [55]. The recontamination, after any cooking or hot water treatments, depends mainly on household conditions (e.g., air, storage containers, spoons, etc.) [72]. In some cases, microbial propagation is guaranteed by the addition of a portion of fermented material from a previous batch (back-slopping).

Environmental parameters such as temperature, pH, inoculum quantity (where applicable), and the fermentation time defines the members of the maize microbiota, which are part of a complex consortium. In addition, the maize pretreatment before fermentation also contributes to the prevalence of some species; in this regard, a greater biodiversity of species and in particular of *Candida* spp. were detected in *chicha*, a Colombian fermented beverage produced with maize pretreated with chewing, compared to those without any treatment [10].

Therefore, as mentioned previously, the mixture of microorganisms that carries out the fermentation leads to a product with very variable quality and sensory characteristics. On the other hand, the geographical isolation among the different fermented maize products provides significantly different microbial communities so that each maize fermented product can be considered as unique [36].

During the fermentation, a given microorganism, or groups of them, initiates the growth and becomes established during a specific period of time; afterward, the growth decreases due to the accumulation of toxic end-products or other inhibitory factors. In this way, the microorganisms provide the appropriate environment to other species less sensitive to those inhibitory factors. Culture-independent approaches have shown that microbial diversity in maize fermented product microbiomes is highly underestimated [11,16,36,53,73]. However, as evidenced in Tables 2 and 3, the coexistence of lactic acid bacteria (LAB) and yeasts in fermented maize products is unavoidable. In addition, the presence of fungi, acetic acid bacteria (AAB), and *Bacillus* species is frequent in several

products. Concerning the pathogenic bacteria, very few studies reported the presence of *Escherichia coli* and *Enterobacter aerogenes*.

Concerning the most common microorganisms found in fermented maize products, it is well established that LAB frequently produce enzymes able to breakdown polysaccharides or other molecules with high molecular weight, as well as organic acids and some compounds able to kill or reduce the microbial populations, such as bacteriocins and hydrogen peroxide [77]. They are also able to increase the content of free amino acids and B group vitamins, improving the availability of iron, zinc, and calcium by breaking down antinutritional compounds [31]; in addition, they produce gas and other volatile compounds (VOCs) contributing to the sensory properties of the product.

Yeasts, besides providing growth factors such as vitamins and soluble nitrogen to LAB, also produce several extracellular enzymes (lipases, esterases, amylases, and phytases), some of which participate in the formation of fermented maize flavor and aroma [45]. Yeasts produce a wide variety of VOCs, such as alcohols, esters, aldehydes, and ketones, that enrich the sensory characteristics of the maize fermented product and also contribute to reducing mold growth and spore germination, as in the case of ethyl acetate [78]. Recently, studies of Ponomarova et al. [79], combining metabolomics and genetics, evidenced that yeasts enable the growth of LAB through endogenous, multi-component cross-feeding in a readily established community.

On the other hand, the aerobic spore-forming bacteria (*Bacillus* spp.) secrete a wide range of degradative enzymes, such as amylases and proteases [80], and can also produce antimicrobial compounds such as bacilysin, which is able to inhibit molds and bacteria; and iturin and chloromethane, which inhibit bacteria [59], thus playing an important role in the fermented maize product development.

During maize fermentation, as occurring in other uninoculated fermentations, the competition among species for substrates, acid tolerance, syntrophic interactions, and other physiological properties of microbial populations causes fast variations in the microbiota structure. However, the microbial consortium of dough and beverages from fermented maize is stable, and mutually beneficial interactions among different species can contribute to the coexistence of some of them [81]. For example, this is the case for *Lactobacillus plantarum*, *Lactobacillus fermentum*, and *Saccharomyces cerevisiae* in ogi [82], *Lb. plantarum* and *Acetobacter fabarum* in masa agria [36], *Pediococcus pentosaceus* and *Weissella confusa* in atole agrio [4] or *Lb. fermentum* and *Lactobacillus delbrueckii* subsp. *bulgaricus* in akamu [2]. Microbiological studies have revealed that during spontaneous fermentation, bacteria and yeasts secrete a diverse array of metabolites that are available for all the community members. Thus, the interactions of the different microorganisms play a significant role during maize fermentation and participate in the changes of the nutritional, rheological, and sensorial traits through modification of the maize composition.

Figure 1 describes the main effect of the metabolic processes of the principal microbial groups involved in maize fermentation, improving their mutual interactions, while Figure 2 depicts the effect of these microbial activities on the characteristics of the final fermented maize. All these activities are detailed in the next paragraphs.

Table 2. Lactic acid bacteria and yeasts involved in the fermentation of maize food products.

Name of Product	Lactic Acid Bacteria	Yeasts	References
Akamu	<i>L. lactis</i> , <i>Lb. acidophilus</i> , <i>Lb. amylovorus</i> , <i>Lb. delbrueckii</i> , <i>Lb. fermentum</i> , <i>Lb. helveticus</i> , <i>Lb. plantarum</i>	<i>C. albicans</i> , <i>C. tropicalis</i> , <i>Candida utilis</i> , <i>Clavispora lusitaniae</i> , <i>Rhodotorula glutinis</i> , <i>Saccharomyces paradoxus</i>	[1,2]
Atole agrio	<i>E. asini</i> , <i>E. casseliflavus</i> , <i>E. faecium</i> , <i>E. hirae</i> , <i>E. mundtii</i> , <i>L. lactis</i> , <i>L. piscium</i> , <i>Lb. aviarius</i> , <i>Lb. brevis</i> , <i>Lb. casei</i> , <i>Lb. composti</i> , <i>Lb. coryniformis</i> , <i>Lb. curvatus</i> , <i>Lb. dextrinicus</i> , <i>Lb. mali</i> , <i>Lb. fabifermentans</i> , <i>Lb. paracasei</i> , <i>Lb. paraplantarum</i> , <i>Lb. plantarum</i> , <i>Lb. pentosus</i> , <i>Lb. rhamnosus</i> , <i>Lc. garlicum</i> , <i>Lc. mesenteroides</i> , <i>Lc. pseudomesenteroides</i> , <i>W. cibaria</i> , <i>W. confusa</i> , <i>W. paramesenteroides</i> , <i>P. stilesii</i> , <i>S. equines</i> , <i>W. hellenica</i> , <i>W. oryzae</i> , <i>P. pentosaceus</i>	u.s.	[4,5]
Busaa	<i>Lb. brevis</i> , <i>Lb. buchmeri</i> , <i>Lb. casei</i> , <i>Lb. helveticus</i> , <i>Lb. plantarum</i> , <i>Lb. salivarius</i> , <i>Lb. viridescens</i> , <i>P. damnosus</i> , <i>P. parvulus</i>	<i>Candida krusei</i> , <i>Saccharomyces cerevisiae</i>	[6,7]
Champús	u.s.	<i>Galactomyces geotrichum</i> , <i>Hanseniaspora sp.</i> , <i>Issatchenkia orientalis</i> , <i>Pichia fermentans</i> , <i>P. kluyveri</i> , <i>Saccharomyces cerevisiae</i> , <i>Torulospora delbrueckii</i> , <i>Zygosaccharomyces fermentati</i>	[9,10]
Chicha	<i>E. durans</i> , <i>E. faecalis</i> , <i>E. faecium</i> , <i>E. gallinarum</i> , <i>E. hirae</i> , <i>E. lactis</i> , <i>E. mundtii</i> , <i>L. lactis</i> , <i>Lb. acidophilus</i> , <i>Lb. aviarius</i> , <i>Lb. brevis</i> , <i>Lb. casei</i> , <i>Lb. composti</i> , <i>Lb. crispatus</i> , <i>Lb. diolivorans</i> , <i>Lb. fabifermentans</i> , <i>Lb. farraginis</i> , <i>Lb. fermentum</i> , <i>Lb. harbinensis</i> , <i>Lb. helveticus</i> , <i>Lb. murinus</i> , <i>Lb. odoratitofui</i> , <i>Lb. paracasei</i> , <i>Lb. paraplantarum</i> , <i>Lb. plantarum</i> , <i>Lb. reuteri</i> , <i>Lb. rossiae</i> , <i>Lb. suebicus</i> , <i>Lb. vaccinostercus</i> , <i>Lc. citreum</i> , <i>Lc. lactis</i> , <i>Lc. mesenteroides</i> , <i>Lc. pseudomesenteroides</i> , <i>S. equinus</i> , <i>S. gallolyticus</i> , <i>W. cibaria</i> , <i>W. confusa</i> , <i>W. hellenica</i> , <i>W. viridescens</i>	<i>Candida parapsilosis</i> , <i>C. zeylanoides</i> , <i>Cryptococcus carnescens</i> , <i>Cry. flavescens</i> , <i>Cry. magnus</i> , <i>Cry. nemorosus</i> , <i>Hanseniaspora uvarum</i> , <i>Debaryomyces hansenii</i> , <i>Kluyveromyces lactis</i> , <i>K. marxianus</i> , <i>Meyerozyma guilliermondii</i> , <i>Pichia sp.</i> , <i>P. fermentans</i> , <i>P. membranifaciens</i> , <i>Rhodotorula mucilaginoso</i> , <i>R. slooffiae</i> , <i>S. cerevisiae</i> , <i>Torulaspota delbrueckii</i> , <i>Wickerhamomyces anomalus</i> , <i>Trichosporon domesticum</i>	[11,12]
Chicha	<i>Lactobacillus sp.</i> , <i>Leuconostoc sp.</i>	<i>Candida ethanolica</i> , <i>C. oleophila</i> , <i>C. parapsilosis</i> , <i>C. pomicola</i> , <i>C. railenensis</i> , <i>C. sergipensis</i> , <i>C. spandovensis</i> , <i>Hanseniaspora opuntiae</i> , <i>H. uvarum</i> , <i>Issatchenkia sp.</i> , <i>Kazachstania exigua</i> , <i>Kodamaea ohmeri</i> , <i>Lodderomyces elongisporus</i> , <i>Metschnikowia korensis</i> , <i>Monilia candida</i> , <i>Mycoderma vini</i> , <i>Oidium lactis</i> , <i>Pichia sp.</i> , <i>P. guilliermondii</i> , <i>Saccharomyces cerevisiae</i> , <i>S. pastorianus</i> , <i>Wickerhamomyces anomalus</i> , <i>W. pijperi</i>	[10]
Chica	<i>Lactobacillus plantarum</i> , <i>Lb. fermentum</i> , <i>Weissella cibaria</i> , <i>Leuconostoc sp.</i> , <i>Lactococcus sp.</i> , <i>S. luteicia</i> , <i>S. alactolyticus</i>		[74]
Doklu	<i>Enterococcus sp.</i> , <i>Lactobacillus sp.</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Pediococcus sp.</i> , <i>P. acidilactici</i> , <i>P. pentosaceus</i> , <i>Streptococcus sp.</i> , <i>Weissella sp.</i> , <i>W. cibaria</i>	u.s.	[13,15]
Gowé	u.s.	u.s.	[18]
Ikii	<i>Lb. confusus</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Lb. rhamnosus</i> , <i>Pediococcus sp.</i>	u.s.	[20,21]
Kachasu	-	u.s.	[7]
Kenkey	<i>Lb. fermentum</i> , <i>Lb. reuteri</i>	<i>Candida kefir</i> , <i>C. krusei</i> , <i>C. mycoderma</i> , <i>C. tropicalis</i> , <i>Saccharomyces cerevisiae</i>	[23]

Table 2. Cont.

Name of Product	Lactic Acid Bacteria	Yeasts	References
Koko	<i>Lb. brevis</i> , <i>Lb. plantarum</i>	<i>Saccharomyces cerevisiae</i>	[7]
Kokoro	<i>Lactobacillus</i> sp.	-	[28]
Mahewu/amahewu	<i>Leuconostoc</i> spp., <i>L. lactis</i> , <i>Lb. delbrueckii</i> , <i>S. lactis</i>	-	[31,32,34]
Masa agria	<i>Lactococcus</i> sp., <i>L. lactis</i> , <i>Lactobacillus</i> sp., <i>Lb. amylolyticus</i> , <i>Lb. brevis</i> , <i>Lb. coleohominis</i> , <i>Lb. delbrueckii</i> , <i>Lb. crustorum</i> , <i>Lb. curvatus</i> , <i>Lb. fermentum</i> , <i>Lb. gallinarum</i> , <i>Lb. helveticus</i> , <i>Lb. nagelii</i> , <i>Lb. nantensis</i> , <i>Lb. panis</i> , <i>Lb. plantarum</i> , <i>Lb. pontis</i> , <i>Lb. rossiae</i> , <i>Lb. siliginis</i> , <i>Lb. vaccinostercus</i> , <i>Lc. citreum</i> , <i>P. argentiniensis</i> , <i>Streptococcus</i> sp., <i>Weissella</i> sp., <i>W. beninensis</i> , <i>W. confusa</i> , <i>W. fabalis</i> , <i>W. fabaria</i> , <i>W. salipiscis</i>	u.s.	[10,36]
Massa	<i>Lb. fermentum</i> , <i>Lb. lactis</i> , <i>Lb. plantarum</i> , <i>Lc. mesenteroides</i> , <i>Pediococcus acidilactici</i>	u.s.	[38]
Mawè	<i>L. lactis</i> , <i>Lb. brevis</i> , <i>Lb. buchmeri</i> , <i>Lb. confusus</i> , <i>Lb. curvatus</i> , <i>Lb. fermentum</i> , <i>Lb. reuteri</i> , <i>Lb. salivarius</i> , <i>Lc. mesenteroides</i> , <i>Pediococcus acidilactici</i> , <i>P. pentosaceus</i>	<i>Candida krusei</i> , <i>Clavispora lusitaniae</i> , <i>Saccharomyces cerevisiae</i>	[16,39,41]
Munkoyo	<i>Lb. brevis</i> , <i>Lb. delbrueckii</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Lb. rossiae</i> , <i>W. cibaria</i> , <i>W. confusa</i>	<i>Saccharomyces cerevisiae</i>	[43,44]
Mutwiwa	<i>Pediococcus pentosaceus</i>	u.s.	[19]
Ogi	<i>E. faecalis</i> , <i>Lb. acidophilus</i> , <i>Lb. brevis</i> , <i>Lb. cellobiosus</i> , <i>Lb. fermentum</i> , <i>Lb. parapantarum</i> , <i>Lb. plantarum</i> , <i>Lc. lactis</i> , <i>Lc. paramesenteroides</i> , <i>P. acidilactici</i> , <i>P. clausenii</i> , <i>P. pentosaceus</i> , <i>S. lactis</i>	<i>Candida albicans</i> , <i>C. krusei</i> , <i>C. tropicalis</i> , <i>C. utilis</i> , <i>Clavispora lusitaniae</i> , <i>Geotrichum candidum</i> , <i>G. fermentans</i> , <i>Rhodotorula glutinis</i> , <i>R. graminis</i> , <i>Saccharomyces cerevisiae</i> , <i>S. pastorianus</i>	[16,45,46,48,49,75]
Pito	<i>Lactobacillus</i> sp.	<i>Candida</i> sp., <i>Geotrichum candidum</i>	[50]
Poto poto	<i>Enterococcus</i> sp., <i>Lb. acidophilus</i> , <i>Lb. casei</i> , <i>Lb. delbrueckii</i> , <i>Lb. fermentum</i> , <i>Lb. gasseri</i> , <i>Lb. plantarum</i> , <i>Lb. reuteri</i>	-	[53,54]
Pozol	<i>Bifidobacterium minimum</i> , <i>Enterococcus</i> sp., <i>E. saccharolyticus</i> , <i>E. sulfureus</i> , <i>Lactococcus</i> sp., <i>L. lactis</i> , <i>Lactobacillus</i> sp., <i>Lb. alimentarius</i> , <i>Lb. casei</i> , <i>Lb. delbrueckii</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Leuconostoc</i> sp., <i>Streptococcus</i> sp., <i>S. bovis</i> , <i>S. macedonicus</i> , <i>S. suis</i> , <i>Weissella</i> sp.	u.s.	[55–60]
Sekete	<i>L. lactis</i> , <i>Lb. brevis</i> , <i>Lb. delbrueckii</i> , <i>Lb. plantarum</i> , <i>Lc. mesenteroides</i> , <i>P. cerevisiae</i> , <i>Streptococcus</i> spp.	<i>Geotrichum</i> sp., <i>Saccharomyces</i> spp., <i>S. cerevisiae</i>	[7,62,76]
Tesguino	<i>Lactobacillus</i> sp., <i>Leuconostoc</i> sp., <i>Pediococcus</i> sp., <i>Streptococcus</i> sp.	<i>Brettanomyces</i> sp., <i>Candida guilliermondii</i> , <i>Cryptococcus</i> sp., <i>Geotrichum</i> sp., <i>Hansenula anomala</i> , <i>Pichia</i> sp., <i>Saccharomyces cerevisiae</i> , <i>S. kluyveri</i>	[63]
Togwa	<i>Lb. brevis</i> , <i>Lb. cellobiosus</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>P. pentosaceus</i> , <i>W. confusa</i>	<i>Candida glabrata</i> , <i>C. pelliculosa</i> , <i>C. tropicalis</i> , <i>Issatchenkia orientalis</i> , <i>Kluyveromyces marxianus</i> , <i>Pichia anomala</i> , <i>Saccharomyces cerevisiae</i>	[64,65]

u.s., unidentified species.

Table 3. Enterobacteriaceae, molds and others bacteria involved in the fermentation of maize food products.

Name of Product	Acetic Acid Bacteria	Enterobacteriaceae	Molds	Others	References
Akamu	-	<i>Enterobacter aerogenes</i> , <i>Escherichia coli</i> , <i>Proteus sp.</i> , <i>Serratia sp.</i>	<i>Aspergillus niger</i> , <i>A. oryzae</i> , <i>Mucor circinelloides</i> , <i>Penicillium citrinum</i> , <i>Rhizopus microsporus</i> , <i>R. oligosporus</i>	<i>Bacillus cereus</i> , <i>B. licheniformis</i> , <i>B. subtilis</i> , <i>Pseudomonas alkaligenes</i> , <i>P. aeruginosa</i>	[1]
Atole agrio	<i>Acetobacter estunensis</i> , <i>A. indonesiensis</i> , <i>A. pasteurianus</i> , <i>A. tropicalis</i> , <i>Gluconacetobacter sp.</i> , <i>Gluconobacter sp.</i> , <i>G. frateurii</i> , <i>Kozakia sp.</i>	u.s.	u.s.	-	[4,5]
Chicha	-	-	<i>Penicillium sp.</i>	-	[12]
Chicha	<i>Acetobacter sp.</i>	-	<i>Aspergillus sp.</i> , <i>Penicillium sp.</i>	-	[10]
Koko	-	<i>Enterobacter cloacae</i>	-	<i>Acinetobacter sp.</i>	[7]
Kokoro	-	<i>Klebsiella sp.</i> , <i>Proteus sp.</i>	<i>Alternaria sp.</i> , <i>Aspergillus sp.</i> , <i>Cephalosporium sp.</i> , <i>Fusarium sp.</i> , <i>Mucor sp.</i> , <i>Penicillium sp.</i> , <i>Rhizopus sp.</i>	<i>Bacillus sp.</i> , <i>Pseudomonas sp.</i> , <i>Staphylococcus sp.</i>	[28]
Masa agria	<i>Acetobacter sp.</i> , <i>A. cibirongensis</i> , <i>A. fabarum</i> , <i>A. lovaniensis</i> , <i>A. orientalis</i> , <i>Gluconobacter oxydans</i>	<i>Enterobacter aerogenes</i> , <i>Escherichia sp.</i> , <i>Pantoea agglomerans</i> , <i>Serratia sp.</i>	-	<i>Acinetobacter sp.</i> , <i>A. junii</i> , <i>A. ursingii</i> , <i>Bacteroides sp.</i> , <i>Comamonas terrigena</i> , <i>Dechloromonas sp.</i> , <i>Delftia</i> , <i>Frateuria aurantia</i> , <i>Gemmata sp.</i> , <i>Pseudomonas sp.</i> , <i>Sphingobium sp.</i> , <i>Sphingomonas sp.</i> , <i>Stenotrophomonas bacterium</i> , <i>Sugarcane phytoplasma</i>	[10,36]
Munkoyo	-	-	-	<i>Bacillus licheniformis</i>	[44]
Ogi	-	<i>Citrobacter sp.</i> , <i>Enterobacter sp.</i> , <i>Escherichia coli</i> , <i>Klebsiella spp.</i>	<i>Aspergillus flavus</i> , <i>A. niger</i> , <i>A. oryzae</i> , <i>Fusarium subglutinans</i> , <i>Mucor circinelloides</i> , <i>Penicillium citrinum</i> , <i>Rhizopus microsporus</i> , <i>R. nigricans</i> , <i>R. oligosporus</i> , <i>R. stolonifer</i>	<i>Acinetobacter berezinae</i> , <i>Aerobacter sp.</i> , <i>Alcaligenes faecalis</i> , <i>Bacillus cereus</i> , <i>B. licheniformis</i> , <i>B. mycoides</i> , <i>B. subtilis</i> , <i>B. thuringiensis</i> , <i>Bordetella avium</i> , <i>B. bronchisepta</i> , <i>Corynebacterium sp.</i> , <i>Micrococcus luteus</i> , <i>Moorella glycerini</i> , <i>Myroides marinus</i> , <i>Pseudomonas aeruginosa</i> , <i>P. hibiscicola</i> , <i>S. aureus</i>	[46,48,49,75]
Pito	-	-	<i>Aspergillus versicolor</i> , <i>Penicillium purpurogenum</i> , <i>P. simplicissimum</i>	-	[50]
Poto poto	-	<i>Escherichia coli</i>	-	<i>Bacillus sp.</i>	[53]
Pozol	-	u.s.	u.s.	<i>Bacillus sp.</i> , <i>Clostridium sp.</i> , <i>Exiguobacterium acetylicum</i> , <i>E. aurantiacum</i> , <i>Oxalophagus oxalicus</i>	[55–57,59,60]
Sekete	-	-	<i>Aspergillus flavus</i> , <i>A. niger</i> , <i>Mucor rouxii</i>	<i>Bacillus subtilis</i> , <i>Propionibacterium spp.</i>	[7,62,76]

u.s., unidentified species.

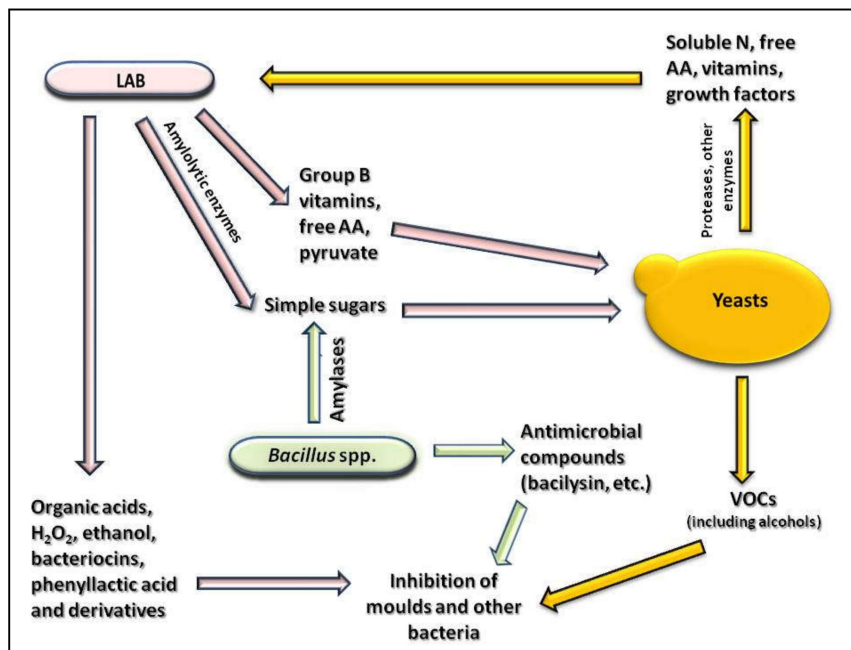


Figure 1. The interactions among the principal microbial groups in maize fermentation.

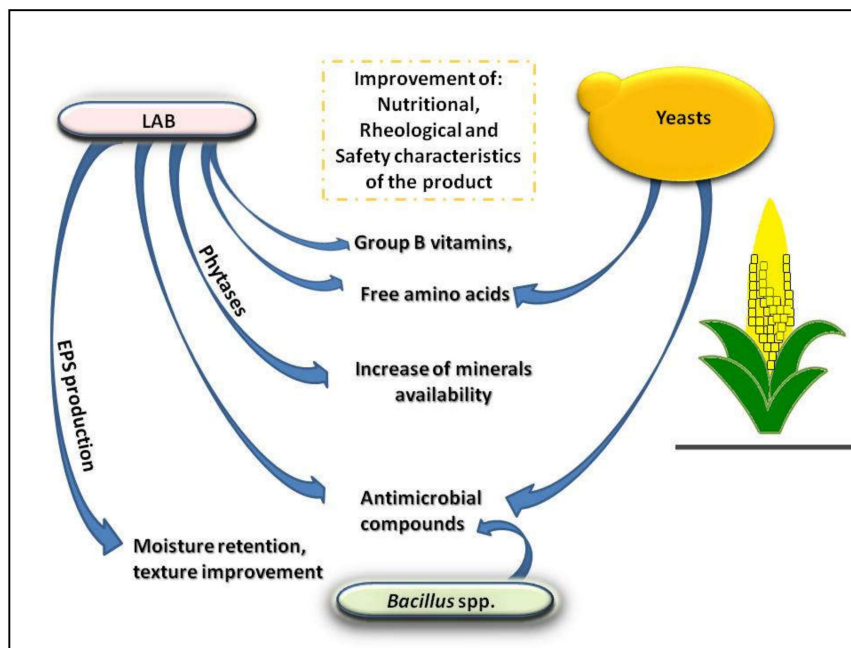


Figure 2. The effect of microbial activities on the characteristics of the final fermented maize product.

3. Production of Amylolytic Enzymes

Mature maize kernels contain low levels of free sugars, mainly generated by endogenous grain amylases; these sugars support the growth of microorganisms like LAB, which can begin the fermentation process [31]. It is well established that at the beginning of maize fermentation, only a few microorganisms are able to use the starch, and for this reason, the microbial biodiversity is lower than in the second stage. The action of microbial amylases releases other carbon sources (i.e., dextrans and maltose) accessible for a greater number of species, including nonamylolytic strains. Moreover, the organic products formed during fermentation (lactic acid, formic acid, and ethanol) may also serve as carbon sources for microorganisms such as yeasts [56]. Thus, the amylolytic activity during

maize fermentation is fundamental because it improves the energy sources for the nonamylolytic microorganisms and plays an important role in the fast reduction of pH values.

The amylolytic activity in LAB species is not a very frequent feature; only a few species exhibit this activity by converting the starch directly into lactic acid in a single step [83]. For this bioconversion, a fundamental role is played by the gene *amyA*, which encodes for an extracellular α -amylase that is not expressed continuously but transiently [84]. In addition, this amylolytic activity is strain-dependent [5] and can be inhibited by the pH reduction due to the lactobacilli growth [85]. In this context, some pre-fermentation processes (Figure 3) could contribute to selecting bacteria with high amylolytic activity [58]. According to Petrova et al. [86], bacteria of *Lactobacillus*, *Lactococcus*, and *Streptococcus* genera are able to directly metabolize starch for the production of lactic acid, with lactobacilli (e.g., *Lactobacillus amylovorus*) as the most efficient.

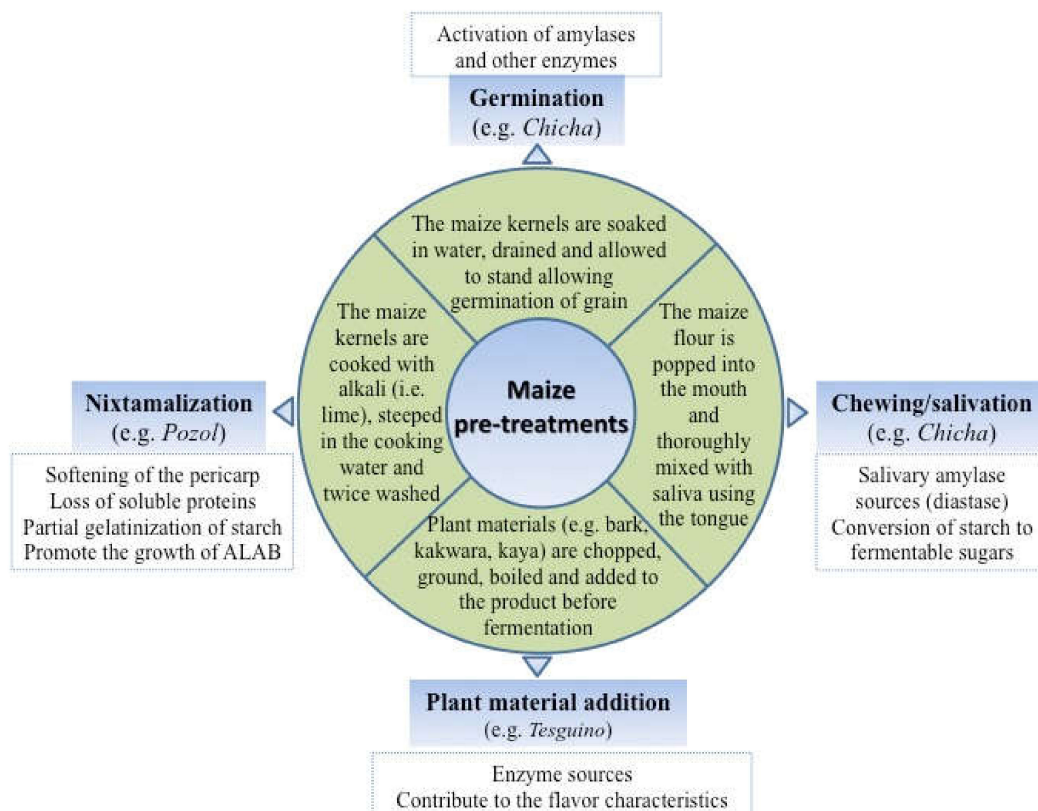


Figure 3. Traditional maize pretreatments.

Amylolytic LAB (ALAB) may be key organisms during the production of the maize fermented food, and this is the case of *Lb. fermentum* in Mexican pozol [56]. In an integrated vision of how the low amounts of fermenting sugars present in maize can determine microbial diversity and support a high number of lactic acid bacteria in pozol, Diaz-Ruiz et al. [58] pointed out that the presence of ALAB in the first stage of fermentation played a fundamental role in this food ecosystem, although their amylase level was low. The authors suggested that the amylolytic activity of *Streptococcus infantarius*, which has been established as a predominant LAB during pozol’s fermentation, together with *Streptococcus bovis*, could provide low-molecular-weight malto-oligosaccharides to the not amylolytic microorganisms during the initial steps of nixtamal dough fermentation. In the same way, *Lb. plantarum* (CPQBA 087–11 DRM) isolated from Colombian masa agria showed high amylolytic activity [87]. The ALAB amylolytic activity is mainly due to the production of extracellular amylases. According to genomic studies, ALAB produce alpha-amylases, maltogenic amylases, amylopullulanases, pullulanases, neopullulanases, and 6-glucosidases [86].

Starch hydrolysis is performed mainly by bacteria rather than by yeasts [88], however, the amylolytic activity was also reported in yeasts as a strain-dependent feature; in particular, *Saccharomyces cerevisiae* (2/77) and *Candida krusei* (2/27), grown in a medium containing amylopectin incorporated with 2% soluble starch, showed high activity [45]. Moreover, *Candida famata*, *C. krusei*, and *S. cerevisiae* isolated from fermented maize in Indonesia and Africa showed amylolytic activity [45, 89]. Chicha from the Andes is a source of yeasts with high amylolytic activity, with *Cryptococcus flavescens*, *Cryptococcus magnus*, *Cryptococcus carnescens*, *Pichia membranifaciens*, *Cryptococcus* spp., *Rhodotorula mucilaginosa*, and *Wickerhamomyces anomalus* as the most potent producers [12,88].

Bacillus spp. bacteria, commonly isolated from fermented maize products, are beneficial as well for the fermentation process due to the production of amylase [90], and particularly of α -amylases, which convert starch to glucose for microorganisms lacking in these enzymes, such as *S. cerevisiae* [91].

The amylolytic activity of bacteria and yeasts is not only beneficial for microbiota growth, but it can also have an effect on the rheology of the product. Acid and amylase enzymes easily attack the amorphous regions of the starch granules, reducing the molecular mass of amylose and amylopectin [92]. This suggests that the enzymes produced by LAB during the maize fermentation have an effect on the glycosidic bonds in the starch granule, hydrolyzing them and enabling the granules to absorb water faster, thus reducing the viscosity of the fermented slurry and the cohesive structure of the doughs. Moreover, while the viscosity of bulk and starchy weaning gruel is decreased, the nutrient density is increased, thus maintaining an acceptable thickness for feeding young children [93].

4. Production of Exopolysaccharides (EPS)

The exopolysaccharides (EPS) are microbial biopolymers secreted into the extracellular environment in the form of capsules or biofilm. These compounds protect the cell against several environmental stresses occurring during fermentation [94], and this encompasses a wide transcriptional response with many induced or repressed genes [95]. Therefore, the particular condition encountered during maize fermentation could favor the production of EPS and could affect the way in which microorganisms interact with the external environment, whether it is liquid or solid [94].

Several factors influence the formation and the features of the different EPS, such as types of monosaccharides, type of linkages, degree of branching, and molecular weight. From the technological point of view, EPS formed from sucrose by glycansucrase activity during sourdough fermentation influence the viscoelastic properties of the dough and beneficially affects the rheological characteristics and shelf-life (in particular starch retrogradation) of the product [96]. In this context, Falade et al. [97], who investigated the impact of fermentation on the maize dough, found a higher elastic modulus than the viscous modulus and suggested that the doughs are viscoelastic solids, exhibiting more elastic properties than viscous ones. Although the authors attributed the cohesive dough structure in sourdough bread in part to endosperm matrix protein degradation, the contribution of EPS to the increase of the viscoelastic nature of the dough should not be underestimated [98]. Moreover, probably the viscous nature of some uncooked products such as ogi and fufu slurries could be partly due to the excretion of exopolysaccharides by the dominant LAB. In addition, EPS confer beneficial physiological effects on human health, such as antitumor activity and immunomodulating bioactivity [99].

EPS-producing LAB belongs to different genera such as *Enterococcus*, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Pediococcus*, *Streptococcus*, and *Weissella*, but also EPS-producers *Bifidobacterium*, *Acetobacter* spp., and *Bacillus* spp. have been reported [100–103]. As reported in Tables 2 and 3, several species of these genera are commonly associated with maize products, and in recent years, the isolation of EPS-producing LAB from spontaneously fermented maize products has gained attention. Some studies suggested that the amount of EPS produced is strain- and species-dependent [100]. On the other hand, Donot et al. [94] suggested that the physiological role of EPS depends on the biotope of the microorganisms producing them.

The roles of EPS produced by LAB have been described by several researchers, nevertheless, the majority of these papers were achieved in lab conditions and using strains growing in

sucrose-containing agar culture. In this context, among 88 strains isolated from atole agrio, *Lb. plantarum* and *P. pentosaceus* were the major EPS producers [5]. In the same way, in a study on 70 LAB strains isolated from ogi, only a few of them, belonging to the species *Lactococcus brevis*, *Lactococcus mesenteroides*, *Lactococcus lactis*, *Lb. fermentum*, *Lactococcus lactis*, and *Lb. plantarum*, showed potential to produce EPS, with values ranging between 120 and 1,390 mg ml⁻¹. EPS production is a common trait of *Lb. plantarum* and *Lactococcus rhamnosus* isolated from Kenyan ikii, with quantities ranging from 298.53 mg l⁻¹ to 431 mg l⁻¹ [21].

Although the exact role of the EPS produced during fermentation on the fermented maize ecosystem is not well elucidated, the presence of EPS in dough could contribute to retaining humidity, delaying water movement through the dough toward the peripheral area, thus reducing the water loss by evaporation. For this reason, the EPS producers could strongly promote the stabilization of dough microbiota.

5. Vitamins and Amino Acids Increase

Maize is often deficient in vitamins (having a very low concentration of vitamins A and B12), and amino acids (lacking arginine and methionine). Some pretreatments of the maize grains, such as germination, contribute to increasing their nutritional value, particularly in terms of peptides, amino acids, vitamins (B1 and E), gamma-aminobutyric acid (GABA), and total phenolic content [104]. Even during fermentation, an increase of some of these compounds occurs. It is generally believed that the yeasts excrete nutrients of which the LAB benefit, such as pyruvate, amino acids, and vitamins. Although LAB are auxotrophic for different growth factors, some strains are able to produce B group vitamins, such as cobalamin (B12), folate (B11), and riboflavin (B2). In particular, some *Lb. plantarum*, *Lactococcus rossiae*, *Lb. fermentum*, *Lactococcus buchneri*, *Lactococcus hilgardii*, and *Lb. brevis* strains were demonstrated to be vitamin B12 producers [105–107], while *Lactococcus pentosus*, *Lb. plantarum*, and *Lactococcus acidophilus* were riboflavin producers. Uninoculated maize fermentation generally increases the levels of nutritional compounds such as thiamine (vitamins B1), folate, riboflavin, total carotenoids, vitamin C, and Vitamin E [27,108–110]. However, the various steps involved in the process of ogi in Cameroon contribute to reducing thiamine (69%), riboflavin (82%), and β -carotene (66%) in maize fermented according to traditional preparation [111]. On the other hand, the increase in folate content has been reported in many fermented products [112]; in fact, it is well established that some indigenous yeasts species such as *S. cerevisiae*, *Candida milleri*, *Torulaspora delbrueckii*, *Issatchenkia orientalis*, *Pichia anomala*, *Kluyveromyces marxianus*, and *Candida glabrata* produce considerable amounts of folate during fermentation. In particular, in togwa, *I. orientalis*, *P. anomala*, *S. cerevisiae*, *K. marxianus*, and *C. glabrata* were able to increase folate concentration after 46 h of fermentation, with *C. glabrata* as the highest producer (23-fold more) compared to unfermented samples [65]. The same authors also highlighted that folate production is highly culture- and species-dependent, being greater during the exponential phase. On the contrary, folate production by LAB is lower, and some of these bacteria deplete folate during fermentation [113]. The increase of methionine, tryptophan, and folate content in fermented maize has also been attributed to the activity of non-LAB-bacteria such as *Bacillus licheniformis* and *Enterobacter cloacae* [114]; again, the ability to synthesize folate may reflect strain differences.

The combined processes of germination and fermentation of maize using *Lactobacillus plantarum*, *Lactococcus lactis*, *Bacillus subtilis*, and *Bifidobacterium longum* increased the content of GABA five-fold. This amino acid could be produced by glutamate decarboxylation performed by *Lactobacillus* spp., and it plays a role in regulating neuronal excitability throughout the nervous system of mammals, inducing hypotension, and exerting diuretic and tranquilizer effects [115].

6. Production of Antimicrobial Compounds

As already described, the fermentation occurring in maize products depends on a consortium of several genera and species. Usually, one or different species start to proliferate and settle down during a specific period of time. Successively, the decrease or even cessation of growth as a consequence

of the increase of toxic end products or other inhibitory factors paves the way to other species less sensitive to those inhibitory factors. Microbial metabolism during maize fermentation may lead to a series of compounds capable of inhibiting a considerable spectrum of bacteria and fungi. In particular, the production of lactic and acetic acids as end products contributes to reducing the pH, creating a hostile environment for the growth of many microorganisms. While lactic acid is produced mainly by LAB, acetic acid is produced principally by acetic acid bacteria (AAB) and specifically by *Acetobacter* spp., when they find excess oxygen [31]. The organic acids disrupt the mechanisms responsible for maintaining the membrane potential, thus inhibiting the active transport across the membrane. In this way, many foodborne pathogens could be inhibited during the fermentative process. In addition, other antimicrobial compounds are recognized to be produced during fermentation, including propionic acid, ethanol generated by yeast, and by LAB via the heterofermentative pathway, H₂O₂ produced during the aerobic growth of LAB, and diacetyl, formed from an excess of citrate-derived pyruvate. Moreover, selected bacteria isolated from fermented maize products display the ability to produce bacteriocins, which are ribosomally synthesized proteinaceous compounds exerting selective antimicrobial activity.

The antimicrobial potential of LAB isolated from fermented maize dough has been studied by Olsen et al. [116], who examined the bacterial interactions during fermentation. They observed a widespread occurrence of antimicrobial compounds, effective against Gram-positive and Gram-negative bacteria. In particular, strains of *Lb. plantarum*, and *Lb. fermentum/reuteri* showed antagonism correlated with the synergic effect of acids, as well as with the production of compounds sensitive to proteolytic enzymes, therefore probably bacteriocins.

In general, in fermented maize, LAB are regularly associated members of the genera *Lactobacillus*, *Pediococcus*, *Leuconostoc*, *Enterococcus*, *Lactococcus*, and *Weissella*, and many species have been recognized as bacteriocin-producers. In one of the first studies in this research field, Olasupo et al. [117] observed a reduction of about 4 log UFC mL⁻¹ of *E. coli* during ogi fermentation, when a bacteriocin-producing *Lactobacillus* was inoculated. Also *Lb. plantarum* E2, isolated from chicha de jora (an alcoholic beverage from Peru), produced a bacteriocin limiting the growth of *Lb. fermentum* Chj4C, another strain isolated from the native beverage [118]. Moreover, 28 strains of *Lb. plantarum* and 3 *Lb. fermentum* isolated from potopoto, produced the bacteriocin plantaricin, able to reduce the population of *Escherichia coli*, *Salmonella enterica*, *Enterobacter aerogenes*, *Bacillus cereus*, *Staphylococcus aureus*, *Listeria monocytogenes*, and *Enterococcus faecalis* [54]. In the same way, one *Lb. rhamnosus* and several *Lb. plantarum* strains isolated from sha'a, a typical maize fermented beverage from Cameroon, produced bacteriocins able to inhibit both Gram-positive and Gram-negative bacteria, including species of the genera *Lactobacillus*, *Streptococcus*, *Bacillus*, *Staphylococcus*, *Salmonella*, *Shigella*, *Pseudomonas*, *Klebsiella*, and *Escherichia*, also including multidrug resistant strains of the pathogens *E. coli* and *S. aureus* [119]. Furthermore, *Lb. lactis*, *Lb. fermentum*, *Lb. casei* and *Lb. plantarum* isolated from ogi, showed different antimicrobial potential, particularly against *Salmonella* Typhimurium and *Shigella dysenteriae* [120]. The potential of *Lb. plantarum* ULAG24 isolated from ogi in Nigeria to release bacteriocins during maize fermentation was exploited to inhibit *Salmonella* in the spot-on-lawn experiment. In this case, the LAB strain expressed all nine genes associated with plantaricin biosynthesis [121]. The inhibition of *E. coli* and *S. aureus* was observed using a bacteriocin-producing *Lactobacillus* isolated from akamu [122].

The high occurrence of bacteriocin-producing *Lb. fermentum* strains, isolated in different stages of doklu production, were reported by Assohoun-Djeni et al. [15]. The authors also observed the capability of 16 strains belonging to various species and mainly *Lb. fermentum*, *Lb. plantarum*, *Pediococcus acidilactici*, *P. pentosaceus*, and *Weissella cibaria* to produce antifungal compounds that inhibited the growth of *Eurotium repens*, *Penicillium corylophilum*, *Aspergillus niger*, *Wallemia sebi*, and *Cladosporium sphaerospermum*. Lactic and acetic acids are the most recognized antifungal molecules produced by LAB, however, other acids such as formic, propionic, butyric, phenyllactic, hydroxyphenyllactic, and indole-3-lactic, in addition to peptides of low molecular weight [123–125] are produced. All of them are supposed to have the fungal cell wall as a target.

The antibacterial activity of *Bacillus* spp. CS93 isolated from pozol has been demonstrated [59,126]; this strain produced several antimicrobial substances such as bacilysin, chlorotetaine, and iturin A, whose efficacy was potent against *E. coli* and *S. aureus*, thus explaining the efficacy of the traditional medicinal uses of pozol by the Mayan civilization [59].

This aspect is very important, as substances produced by several bacteria to protect themselves and to maintain a competitive advantage on other microorganisms not only contribute to the succession dynamics of the different microbial groups but also improve the microbiological quality and safety traits of this kind of products.

7. Reduction of Phytates

As with other cereal grains, maize contains some antinutritional factors such as phytic acid (PA) or phytate (PI) as salt, polyphenols, and tannins that can cause serious problems to human health. In fact, by forming a complex with minerals and by enzymes inhibition, phytic acid reduces the bioavailability and digestibility of proteins and carbohydrates. PA is myo-inositol 1,2,3,4,5,6-hexakis (dihydrogen phosphate), and it is the principal storage form of phosphorus and inositol in several oil seeds and grains [127]. It accounts for 50–80% of the total phosphorous, particularly in maize, with the greater part of PA (>80%) concentrated in the germ. Untreated PA has the ability to chelate important cations such as Ca^{2+} , Mg^{2+} , Fe^{2+} , and especially Zn^{2+} , and residues of proteins, forming a very insoluble salt in which the minerals are very little bio-available as well. The phytases reduce the hexa form of phytic acid (IP6; myo-inositol 1,2,3,4,5,6-hexakisphosphate) into lower forms, such as IP5, IP4, IP3, IP2, IP1, and myo-inositol [128]. The lower forms of PA have a lower binding capacity for metals such as iron and zinc [129].

Phytic acid not only has negative health effects as it chelates important minerals but also because it impairs the absorption of lipids and proteins due to the inhibition of the enzymes pepsin, amylase, and trypsin [130]. In fact, some food processing can partially degrade PA [131], however, most of the food phytate remains not degraded and reaches the gastrointestinal tract, where gut microbiota is usually not efficient in expressing phytate-degrading enzymes (phytases). In this context, Markiewicz et al. [132] suggested that the efficacy of the phytate degradation improves when the microbiota is already adapted to a high content of phytate, as occurs in the vegetarians' intestine.

The potential antinutritional effects of PI present in maize is, to some extent, limited by the fermentation process, which is one of the most effective measures to reduce its amount. In fact, during cereal fermentation, endogenous and microbial phytases find optimum pH conditions for their activities, therefore releasing minerals such as manganese (which is an important growth factor for LAB), iron, zinc, and calcium [31]. In particular, natural fermentation of maize can achieve a significant reduction in PI; for example, Ejigui et al. [111] showed a PI reduction of 61% in corn flour after 96 h of fermentation at 30 °C. Recently, Gabaza et al. [133] observed a reduction between 20% and 88% of phytic acid in slurries maize samples from five different locations in Zimbabwe, after 26 h of fermentation. The authors also observed an increase of iron and zinc bioaccessibility, correlated in part with the reduction of phytic acid. The hypothesis that microorganisms involved in maize fermentation constitute the active part in maize detoxification was supported by early studies in vitro [134]. The authors demonstrated that *Bacillus subtilis*, *B. cereus*, *B. licheniformis*, *Bacillus megaterium*, *Pseudomonas maltophyla*, and *Pseudomonas aeruginosa* isolated during maize fermentation were able to reduce the phytate-phosphorous up to 68%. Successively, many authors have reported positive results in the reduction of PI using lactic acid bacteria and yeasts, improving the bioavailability of minerals in fermented maize [135,136]. The reduction of phytic acid by the natural microbiota has also been reported during the fermentation of maize bran by Decimo et al. [137]; in this case a reduction of 50% at the end of the sourdough-like fermentation process (corresponding to the twelfth refreshment), was reported.

It has been suggested that starter cultures are more effective than natural contaminants in uninoculated fermentation in reducing the PI content [138]. The ability of a lactic acid fermenting

system in decreasing the phytate amount of fermented maize is dependent on various characteristics, as well as on environmental conditions during growth, harvest and storage of the cereal. Fermentation of maize flour resulted in an 88% reduction of phytic acid, and even lower levels of phytic acid remained when a starter culture (61%) or a germinated flour (71%) were used [139]. In this context, positive results were obtained with *Lactobacillus amylovorus* that has been demonstrated to be a good phytase producer in the defined MRS medium supplemented with 1% glucose and 24 mg of PI [140], and with *L. buchneri* M11 that reduced the PI content up to 95.5% after 72 h at 30 °C in kutukutu (from Cameroon). In addition, the levels of calcium, potassium, magnesium, sodium, sulphur, and zinc were significantly ($p < 0.05$) increased in amaku (from Nigeria) fermented with *L. plantarum* strains [3]. The capability of selected yeast, isolated from fermented dough and beverages, to reduce the PI content has been also reported, in particular for *P. kudriavzevii*, *S. cerevisiae*, *Candida tropicalis* and *Pichia kluyveri* [141,142].

Some yeast strains originating from togwa seemed to have developed a high phytase production; particularly *Pichia kudriavzevii* TY13 and *Hanseniaspora guilliermondii* TY14 [143] showed a great myo-inositol hexakisphosphate (IP6) degrading capacity during fermentation in maize-based model togwa, being able to degrade about 95% of the initial phytate amount. *S. cerevisiae*, *C. krusei*, *C. tropicalis*, and *G. candidum* were also able to degrade phytate.

During fermentation, other metabolic pathways are involved in the production of several interesting bioactive molecules. For example, phenolic compounds such as phenolic acids, flavonoids, and tannins, deriving from whole grain cereals, could be metabolized by microorganisms and modified into higher bioactive compounds (i.e., catechin, quercetin, and gallic acid) [144]; these and other microbial-based transformations are worthy of investigation.

8. Reduction of Mycotoxins

Mycotoxins are fungal metabolites commonly occurring in food, which pose a health risk for consumers. Maize is considered the most susceptible crop to mycotoxin contamination. In particular, aflatoxins (AFs), cyclopiazonic acid (CA), fumonisins (FUM), and zearalenone (ZEN) are the most frequent mycotoxins revealed in maize [145], although other mycotoxins such as cereulide and patulin have been reported in maize products [146]. It is well known that maize contamination with mycotoxins can occur either during pre-harvest, when the crop plant is growing, or during post-harvest processing. Mycotoxins are very stable to the physical and chemical treatments used in food processing, thus their elimination is very difficult; nevertheless, some processes, such as cleaning, milling, brewing, fermentation, cooking, baking, frying, roasting, flaking, alkaline cooking, nixtamalization (soaking, cooking in an alkaline solution, and hulling of grains), and extrusion [147] have been shown to reduce the mycotoxin content. During fermentation, maize detoxification can be achieved by microbial binding and/or biotransformation of mycotoxins into less toxic compounds [148]. Several strains of lactic acid bacteria and yeasts exhibit detoxifying properties, and their potential in removing mycotoxins has been reported [149]. This capability has been associated with the noncovalent binding of mycotoxins by fractions of the cell wall skeleton of lactic acid bacteria and yeasts [150]. On the basis of several studies, it appeared that pH and temperature influenced the binding, pH 4 and 37 °C being the most favorable conditions, although with differences among the strains [151]. Some mycotoxins (e.g., AFB1, FB1, and ZEN) were proven to be degraded to various extents by fermentation or biotransformation during maize fermentation processes. In this context, the aflatoxin B1 removal can occur due to the opening of AFB1 lactone ring, resulting in its complete detoxification [152].

The individual or synergistic activity of lactic acid bacteria or yeast strains applied as starter cultures has also been explored to reduce the mycotoxin content in maize products. In general, efficient detoxification can be achieved by the deliberate introduction of lactic acid bacteria strains. Table 4 reports some examples of the species used and the related mycotoxins reduction achieved.

The results of these studies indicate that lactic acid bacteria and some yeast species showed a good performance in reducing the mycotoxin content. In addition, as suggested by Cho et al. [161] and

Haskard et al. [162], mycotoxins degradation during fermentation may either be strain-specific or may require synergistic interactions of more than one species/strain. Moreover, other non-LAB species (e.g., *Bacillus subtilis*) have been implicated in ZEN degradation (up to 99% of 1 mg/kg after 24 h) in liquid medium [75,163]. An excellent review documenting the decontamination of mycotoxins in fermented foods is available in the literature [163] and can be consulted for further information.

Table 4. Reduction of mycotoxins (%) during fermentation.

Mycotoxin	Detoxifying Microorganism	Reduction (%)	Strain Origin	Place of Fermentation	Reference
Aflatoxin B1	Indigenous microbial communities	40–60.8	Ogi	Ogi	[55]
		27.5	Maize meal	Maize meal	[153]
	<i>Lb. brevis</i>	63	Kutukutu	Kutukutu	[30]
	<i>Lb. buchneri</i>	64.2	Kutukutu	Kutukutu	[30]
	<i>Lb. rhamnosus</i> and <i>S. thermophilus</i>	92–100	Commercial strains	Kwete	[154]
	<i>S. lactis</i> and <i>Lb. delbrueckii</i>	75	Commercial strains	Maize meal	[145]
Aflatoxin B2	Indigenous microbial communities	68–82.8	Ogi	Ogi	[55]
	<i>Lb. rhamnosus</i> and <i>S. thermophilus</i>	91.8–100	Commercial strains	Kwete	[154]
Aflatoxin M1	Indigenous microbial communities	100	Ogi	Ogi	[55]
Aflatoxins	Indigenous microbial communities	80	Ogi	Ogi	[153]
		≥91	Mawe	Mawe	[153]
	<i>Lb. acidophilus</i>	37.5	Ogi	Maize	[155]
	<i>Lb. brevis</i>	75	Ogi	Maize	[155]
	<i>Lb. casei</i>	62.5	Ogi	Maize	[155]
	<i>Lb. delbrueckii</i>	56.25	Ogi	Maize	[155]
	<i>Lb. plantarum</i>	95	Ogi	Maize	[155]
Alternariol	Indigenous microbial communities	96.7	Kunu-zaki	Kunu-zaki	[156]
Alternariolmethylether	Indigenous microbial communities	96	Kunu-zaki	Kunu-zaki	[156]
Beauvericin	Indigenous microbial communities	99.9	Kunu-zaki	Kunu-zaki	[156]
Citrinin	Indigenous microbial communities	33–100	Ogi	Ogi	[75]
Cyclopiazonic acid	Indigenous microbial communities	98.1–100	Ogi	Ogi	[75]
Deoxynivalenol	Indigenous microbial communities	98.9	Kunu-zaki	Kunu-zaki	[156]
Enniatins	Indigenous microbial communities	94.7	Kunu-zaki	Kunu-zaki	[156]

Table 4. Cont.

Mycotoxin	Detoxifying Microorganism	Reduction (%)	Strain Origin	Place of Fermentation	Reference
Fumonisin B1	Back slopped*	30	Maize based porridge	Maize based porridge	[157]
		68	Togwa	Togwa	[158]
	Indigenous microbial communities	20	Maize based porridge	Maize based porridge	[157]
		55	Togwa	Togwa	[158]
		13–88.8	Ogi	Ogi	[75]
		99.4	Kunu-zaki	Kunu-zaki	[156]
	24.4	Maize meal	Maize meal	[159]	
	<i>Lb. casei</i>	17	n.a.	Maize based porridge	[157]
		52	n.a.	Togwa	[158]
	<i>Lb. delbrueckii ssp. delbrueckii</i>	69	Ogi and mahewu	in vitro: 24 h, 30°C, pH 4	[150]
		29	Ogi and mahewu	in vitro: 6 d, 30°C, pH 4	[150]
	<i>Lb. fermentum</i>	17	n.a.	Maize based porridge	[157]
		55	n.a.	Togwa	[158]
	<i>Lb. plantarum</i>	73	Ogi and mahewu	in vitro: 24 h, 30°C, pH 4	[150]
		8	Ogi and mahewu	in vitro: 6 d, 30°C, pH 4	[150]
		24	n.a.	Maize based porridge	[157]
		55	n.a.	Togwa	[158]
	<i>Pediococcus pentosaceus</i>	43	Ogi and mahewu	in vitro: 24 h, 30°C, pH 4	[150]
		19	Ogi and mahewu	in vitro: 6 d, 30°C, pH 4	[150]
		24	n.a.	Maize based porridge	[157]
45		n.a.	Togwa	[158]	
	<i>S. lactis</i> and <i>Lb. delbrueckii</i>	74.6	Commercial strains	Maize meal	[159]
Fumonisin B2	Indigenous microbial communities	44–80	Ogi	Ogi	[75]
	<i>Lb. delbrueckii ssp. delbrueckii</i>	95	Ogi and mahewu	in vitro: 24 h, 30 °C, pH 4	[150]
		6	Ogi and mahewu	in vitro: 6 d, 30 °C, pH 4	[150]
	<i>Lb. delbrueckii ssp. bulgaricus</i>	55	n.a.	in vitro: corn infusion, 24 h, 25°C, pH 4	[152]
	<i>Lb. plantarum</i>	95	Ogi and mahewu	in vitro: 24 h, 30 °C, pH 4	[143]
		21	Ogi and mahewu	in vitro: 6 d, 30 °C, pH 4	[143]
	<i>Lb. rhamnosus</i>	80	n.a.	in vitro: corn infusion, 24 h, 25 °C, pH 4	[160]
	<i>Leuconostoc mesenteroides</i>	65	n.a.	in vitro: corn infusion, 24 h, 25 °C, pH 4	[160]
	<i>Pediococcus pentosaceus</i>	89	Ogi and mahewu	in vitro: 24 h, 30 °C, pH 4	[150]

Table 4. Cont.

Mycotoxin	Detoxifying Microorganism	Reduction (%)	Strain Origin	Place of Fermentation	Reference
		67	Ogi and mahewu	in vitro: 6 d, 30 °C, pH 4	[150]
Fumonisin B3	Indigenous microbial communities	46–95	Ogi	Ogi	[55]
Fumonisin	Indigenous microbial communities	99.5	Kunu-zaki	Kunu-zaki	[148]
		29	Ogi	Ogi	[146]
		≥87	Mawe	Mawe	[146]
Fusaproliferin	Indigenous microbial communities	97.8	Kunu-zaki	Kunu-zaki	[148]
Moniliformin	Indigenous microbial communities	98.3	Kunu-zaki	Kunu-zaki	[148]
Zearalenone	Indigenous microbial communities	79–100	Ogi	Ogi	[75]
		76.2	Kunu-zaki	Kunu-zaki	[156]
		34.3	Maize meal	Maize meal	[159]
	<i>Lb. delbrueckii ssp. bulgaricus</i>	75	n.a.	in vitro: corn infusion, 24 h, 25 °C, pH 4	[160]
	<i>Lb. rhamnosus</i>	80	n.a.	in vitro: corn infusion, 24 h, 25 °C, pH 4	[160]
	<i>Leuconostoc mesenteroides</i>	75	n.a.	in vitro: corn infusion, 24 h, 25 °C, pH 4	[160]
	<i>S. lactis</i> and <i>Lb. delbrueckii</i>	68.2	Commercial strains	Maize meal	[159]

* back-sloped is referred to practice based on the inoculation of material coming from a previous batch culture.
n.a., not available.

9. Conclusions

During maize fermentation, as in other natural fermentation, the competition among species for substrates, the acid tolerance, the syntrophic interactions, and other physiological properties of microbial populations cause variations in the microbiota structure. The studies have revealed that natural microbiota produces a wide assortment of compounds that are made accessible for all the community members, also inducing changes of the nutritional, rheological and sensorial treats of the fermented product, and with undeniable positive effects on the consumers, by the reduction of undesirable compounds and the improvement in vitamin and mineral availability.

Through spontaneous fermentation, the maize, a relatively poor cereal, can be transformed into a rich product, as the basis of the diet for many populations all over the world. However, because of the complexity of the microbiota and of the interactions occurring between microorganisms and maize environment, the role of the single microbial groups on the product is not always very obvious. In fact, although in the last years more attention has been paid to the microbiota of fermented maize products, it is important to deeply study the role particularly of subdominant populations, in order to better understand the processes that shape and drive the composition and dynamics of the maize fermentation as an essential step, not only to improve the process but also to safeguard human health.

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