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Microbial-based biofortification to mitigate African micronutrients deficiency: A focus on plant-based fermentation as source of B-group vitamins

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ABSTRACT

Micronutrient deficiency is a form of malnutrition responsible for different metabolic diseases, widely shared among developing low-and middle-income African countries. While deficiencies of calcium, iron, vitamin A, zinc, and selenium have been counteracted mainly by implementing mandatory food fortification programs, little attention was given so far on strategies to decrease inadequate intake of water-soluble B-group vitamins. In this review, we summarize the physiological role of B-group vitamins, and discuss the approaches commonly used to tackle their deficiencies in Africa, namely (i) dietary diversification, (ii) supplementation, and (iii) fortification, with the main focus being here the microbial-based biofortification of food. We report the increasing evidence of plant-based African fermented foods as important sources of these vitamins and how microbial-based biofortification strategies may enhance their content and bioavailability during plant-based fermentation, especially seen for folate (vitamin B9), riboflavin (vitamin B2), and cobalamin (vitamin B12). The selection of pro-technological functional microbial strains from spontaneous fermentation and/or unconventional food matrices, the employment of vitamin overproducing lactic acid bacteria, as well as the implementation of adequate food processes are promising tools that could be implemented in the production of staple home-made fermented foods to counteract B-group vitamins deficiencies. Further research is needed to explore the biotechnological potential of underexploited indigenous microbial strains and the impact of fortified foods on gut host health.

1. Introduction

The World Health Organization (WHO) provides a tripartite classification of malnutrition, i.e. undernutrition, micronutrient deficiency and over-nutrition such as obesity and overweight (Scrinis, 2020). Among them, micronutrient malnutrition can emanate from an imbalance intake or absorption.

Micronutrients are both inorganic minerals (e.g iron, calcium, zinc) and organic compounds (e.g. vitamins) essential for the physical and mental development and for the correct functioning of the immune system (Kennedy, Nantel, & Shetty, 2003; Lukaski, 2004). Such compounds play key roles in human metabolism acting as i) cofactors involved in enzyme activity modulation; ii) coenzymes playing an active role in essential biochemical reactions; iii) transcription control factors binding DNA and regulating the transcription of steroid hormone receptors and other factors; iv) antioxidants and stabilizers protecting cells and tissues against free radicals and peroxides (Godswill, Somtochukwu, Ikechukwu, & Kate, 2020; Hercberg et al., 2004).

Micronutrients deficiency is a threat to human health worldwide, with particular reference to vulnerable subjects such as children and pregnant women in low-income countries (Stevens et al., 2022). Even a short time of intense micronutrient malnutrition in the uterus or during

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early childhood can permanently impair a child's future physical ability, cognitive capacity and economic productivity, consequently give rise to permanent damage. Irreversible cognitive and physical impairment engender poverty traps where they permanently devalue human capital (Barrett & Carter, 2013). Approximately 2–3 billion people worldwide are estimated to suffer from micronutrient deficiencies, especially in developing countries. However, most of the micronutrient deficiencies are chronic, with no clinical sign and are thus commonly refer to as "hidden hunger". Therefore, the global prevalence of people with micronutrient deficiencies remains undiagnosed and their occurrence probably underestimated (Kolahdooz, Spearing, & Sharma, 2013; Manjeru, Van Biljon, & Labuschagne, 2019; Stevens et al., 2022). Moreover, even though there are 29 known essential micronutrients, only a few of them including iron, zinc, vitamin A, and vitamin D are generally analyzed in representative surveys (Stevens et al., 2022) while in most studies the estimation of micronutrient deficiencies are indirectly deduced based on the prevalence of typical diseases such as anaemia, or by data on the food availability. For example, recent assessment showed that low-income countries, wherein typical diets mainly include the consumption of roots and cereal-based products, often lack in important micronutrients such as choline and cobalamin (Chen, Chaudhary, & Mathys, 2021).

In the last years, several approaches have been proposed with the aim of improving the essential micronutrient contents of staple foodstuffs by mandatory food fortification programs worldwide (Conti, Kalmpourtzidou, Lambiase, De Giuseppe, & Cena, 2021; Ohanenye et al., 2021). Fortification programs in sub-Saharan Africa contributed to an increase in the intake of iron, vitamin A, and zinc, but only moderately of some B-group vitamins such as folate, cobalamin, and riboflavin (Beal, Massiot, Arsenault, Smith, & Hijmans, 2017). Other strategies, such as selective breeding have also been proposed to support biofortification of some crops with vitamin A, selenium and zinc, and promising healthy benefits have been reported in Zambia (Galani, Orfila, & Gong, 2022; Roorkiwal, Pandey, Thavarajah, Hemalatha, & Varshney, 2021). However, these approaches are often not available in African countries, and their application may increase the cost of food in an unsustainable way for low-income families (Pasricha et al., 2020).

It is well-known that fermentation of plant-based matrices contribute to enhance the traditional dietary diversity, increasing the quality attributes of the raw materials at different levels (i.e. nutritional, functional and organoleptic) as well their safety and shelf life (Owusu-Kwarteng, Agyei, Akabanda, Atuna, & Amagloh, 2022). In particular, microbial biofortification based on the employment of selected strains able to produce higher levels of specific vitamins could be a suitable alternative to improve the vitamin B content of raw matrices during the fermentation process, in a compatible way with sustainable productions at small industrial scale or household levels (Banwo, Oyeyipo, Mishra, Sarkar, & Shetty, 2022; Misci et al., 2021).

In this review, we provide an overview on B-group vitamins with a focus on their physiological role, deficiency, as well as their occurrence in the main typology of plant-based African fermented foods. We moreover report the general approaches to mitigate micronutrients deficiencies in Africa. A special focus is given here on microbial-based biofortification approaches as a valuable tool to enhance the content and bioavailability of the B-group vitamins to critically discuss the state-of-the-art and the implementation of innovations in food biofortification as alternative sustainable to mitigate malnutrition events in African countries.

2. Vitamin deficiencies in Africa

Humans lack the ability to synthesize vitamins on a sufficient level; therefore, they must be obtained either from dietary sources or possibly from microbial production in the gut (LeBlanc et al., 2013). Based on their different solubility, vitamins are known as fat-soluble (namely vitamins A, D, E and K) and water-soluble (vitamin C and B-group vitamins: thiamin or vitamin B1; riboflavin or vitamin B2; niacin or vitamin B3; pantothenic acid or vitamin B5; pyridoxine or vitamin B6; biotin or vitamin B7; folate or vitamin B9 and cobalamin or vitamin B12) (Zempleni, Suttie, Gregory, & Stover, 2013). A summary of all vitamins, their physiological roles for human health, the food sources and Recommended Daily Amount (RDA) is given in Table 1.

Vitamin deficiencies occur when intake and absorption of vitamins are lower than RDA to sustain good health status, and can be result in severe, devastating, and life-threatening conditions (Balakrishna, Manda, Mwambi, & van Graan, 2021). Among micronutrient deficiencies, those derived from B-group vitamins can cause an array of serious diseases (Titcomb, Schmaelzle, Nuss, Gregory, & Tanumihardjo, 2018), as reported in details in Table 1.

In Africa, robust data on the epidemiology of B-group vitamins deficiencies are limited, probably due to the inhomogeneity of representative biomarker data for micronutrient status of the population, and they have so far received little attention both from public health and clinical perspectives (Stevens et al., 2022). Available data on the prevalence of reported deficiency of B-group vitamins in Africa are listed in detail in Table 2. Briefly, prevalence of thiamin deficiencies ranged from 23 to 64% among adults and men in Cote'd Ivoire, Somalia, Nigeria and other Western Africa countries (Aké-Tano et al., 2011; Watson et al., 2011; Whitfield et al., 2018). Moreover, thiamin deficiency has been reported commonly spread in many African countries, affecting up to a third of children and women of child-bearing age (Keating, Johnson, Cardiel Nunez, & Fischer, 2023). For riboflavin the prevalence of 65 and 49.6% was reported among children under 5 years of age in Cote'd Ivoire and Uganda respectively, in the years 2004–2009 (Nichols et al., 2013; Rohner, Zimmermann, Wegmueller, Tschannen, & Hurrell, 2007). In South Africa, a report was given about the deficiency of niacin among children under five years of age (6%) and women of reproductive age (29.4%), however, there are little or no information about the incidences of pantothenic acid, pyridoxine, and biotin in Africa.

Micronutrient surveys in African countries indicated a high burden of folate and cobalamin deficiency among women of reproductive age. In particular, folate deficiency was highly prevalent in Cameroon (35%), Cote d'Ivoire (91%), Ethiopia (32%) and Ghana (59%). The worse condition of cobalamin deficiency was observed in Malawi, with 54% of women having cobalamin depletion or deficiency, while in Kenya and Ethiopia, 35% and 15% were deficient. In contrast, a relatively lower prevalence (7%) was reported in Ghana (Gebremedhin, 2021).

A recent survey indicated a high prevalence of vitamin B deficiency for non-lactating women (22%–78% depending on the vitamin B) that ranged among 28%–99% for lactating women. In particular, a percentage of about 74%–78% and 91%–99% for non-lactating and lactating women, respectively, not meet their needs for thiamin, riboflavin and folate (Kaliwile et al., 2019).

3. Strategies to mitigate vitamin deficiencies

Globally, the main strategies adopted to address vitamin deficiencies challenges are (i) dietary diversification, (ii) supplementation, and (iii) fortification (Bhutta, Salam, & Das, 2013) (Fig. 1).

3.1. Dietary diversification

A diverse and balanced diet encompasses plant and animal-based commodities, which lineate an ideal panacea to furnish all-inclusive nutrients. Structuring and consuming such diets restrain micronutrient malnutrition as well as a spectrum of non-communicable diseases (Baye & Kennedy, 2020). However, in African countries a major cause of malnutrition is the low diet diversity. In particular in poor rural households, diets consist mainly of starchy staples, such as maize, rice, cassava, and yams and sugary beverages (Korir, Rizov, & Ruto, 2023). In contrast, a lower consumption of meat and dairy products than European countries has been reported (Saubade, Hemery, Guyot, & Humblot,

Table 1

Overview of the main physiological roles for human health, most common symptoms of deficiency, the main food sources and the Recommended Dietary Allowance (RDA) of fat-soluble and water-soluble vitamins.

Vitamin	Physiological roles	Deficiency symptoms	Main food sources	RDA[a]	References
Fat soluble vitamins					
Vitamin A	Bone growth, tooth development, reproduction, cell protection and division, gene expression, immune system regulation	Night blindness, xerophthalmia, and an increased risk of mortality in children and pregnant women	Dairy products, fish and liver, and some fruits and vegetables, especially orange or dark green	900 μg/day (adult male), 700 μg/day (adult female), 770 μg/day (pregnancy), 1300 μg/day (lactation)	(Celep, Kaynar, & Rastmanesh, 2017; Duester, 2000; Maoka, 2020)
Vitamin D	Bones, teeth and muscles development	Rickets (inadequate bone mineralization), osteomalacia, osteoporosis (low bone density and bone tissue deterioration) and colorectal cancer	Cod liver oil, goat milk, egg yolk, butter, sea fish, mushrooms, and avocado	15–20 μg/day for adult males and adult females	(Bier, Mann, Alpers, Vorster, & Gibney, 2014; Holick, 2004; Spiro & Buttriss, 2014)
Vitamin E	Prevention of the oxidation of tissue membranes and lipoproteins; strengthenment the immune system, regulation of cholesterol and hormone levels. Involved in anti-inflammatory events, cell renewal, and protection against free radicals	Amblyopia (lazy eye), muscle atrophy, infertility, muscle dystrophy, hemolysis, and peripheral neuropathy degeneration of axons	Green peppers, cabbage, spinach, flaxseeds, nuts, avocado, olives, sunflower and safflower oil, and other oily foods	15 μg/day (adult male, adult female, pregnancy), 19 μg/day (lactation).	(Bier et al., 2014; Rizvi et al., 2014)
Vitamin K	Healthy blood clotting, activation of bone formation proteins, helping the functionality of blood, bones, and kidneys	Haemorrhaging/blood clotting disorder	Green leafy vegetables, broccoli, eggs, onions, oats, tomatoes, peas, caulis, and vegetable oils	120 μg/day (adult male), 90 μg/day (adult female and pregnancy), 19 μg/day (lactation)	(Di Nicolantonio, Bhutani, & O'Keefe, 2015)
Water-soluble vitamins					
Thiamin (vitamin B1)	Treatment of liver damage and inefficiency, maintenance of proper nervous system function	Beriberi (cardiac and neurologic), Wernicke and Korsakov syndromes (alcoholic confusion and paralysis)	Whole grains, fermented cereals, bread, pasta, rice, tortillas, *garri*, *mahewu*, *kunun-zaki*, *ugba*, *ogiri* and *nono*	1.4 mg/day (adult male), 1.1 mg/day (adult female), 1.5 mg/day (pregnancy), 1.6 mg/day (lactation).	(Bayata, 2019; Johnson et al., 2019; Okwunodulu & Agha, 2020; Polegato et al., 2019)
Riboflavin (vitamin B2)	Key component of coenzymes involved with the growth of cells, energy production, and the breakdown of fats, steroids, and medications	Fatigue, eye changes, dermatitis on the nose and lips, brain dysfunction, impaired iron absorption, brittle nails, and mouth lacerations	Liver, eggs, dark green vegetables, legumes, whole and enriched grain products, milk, *garri* and African fermented vegetable proteins such as *iru*	1.3 mg/day (adult male), 1.1 mg/day (adult female), 1.4 mg/day (pregnancy), 1.6 mg/day (lactation).	(Bayata, 2019; Hrubša et al., 2022; Olanbiwoninu et al., 2017)
Niacin (vitamin B3)	Involvement in energy production, normal enzyme function, digestion, normal appetite, healthy skin and nerves	Pellagra (inflammation of the mucous membranes, skin lesions, diarrhoea and neurological disorders)	Animal products such as liver, fish, poultry, meat, peanuts, whole and fermented grain products such as *ogi*	16 mg/day (adult male), 14 mg/day (adult female), 18 mg/day (pregnancy), 17 mg/day (lactation).	Akinsola, Alamu, Otegbayo, Menkir, and Maziya-Dixon (2021)
Pantothenic acid (vitamin B5)	Involvement in energy production, hormone formation, and dietary fats, proteins, and carbohydrates breakdown. It prevents greying, alopecia, skin and mucosa disorders	Uncommon due to its wide availability and ubiquitous distribution in most foods	Liver, kidney, heart, meats, yeasts, egg yolk, asparagus, peas, mushrooms, sunflower seeds, watermelons, whole grains, legumes, and *mahewu* (a fermented maize (corn)-based non-alcoholic beverage)	5 mg/day (adult male), 7 mg/day (adult female).	(Hrubša et al., 2022; Obafemi et al., 2022; Said, 2014)
Pyridoxine (vitamin B6)	Metabolism of carbohydrates, lipids, amino acids, and nucleic acids. Involved in the production of chemicals such as insulin and haemoglobin for red blood cell formation. Beneficial for motion sickness, nerve pain, liver damage, premenstrual syndrome, protein digestion. Essential during pregnancy when combined with folic acid.	Skin disorders, dermatitis, cracks at the corners of the mouth, anaemia, neurological disorders, convulsions, anaemia, elevated plasma homocysteine kidney stones, and nausea. Deficiency in infants can cause mental confusion	Pork, meats, whole grains and cereals, legumes, and green leafy vegetables, *mahewu* (a fermented maize (corn)-based non-alcoholic beverage) and *ogiri* (a fermented condiment)	2.0 mg/day (adults), 1.6 mg/day (pregnancy), 2.1 mg/day (lactation).	(Arukwe & Onyeneke, 2020; Calderón-Ospina & Nava-Mesa, 2020; Celep et al., 2017)
Biotin (vitamin B7)	Promotion of the release of energy from carbohydrates and the metabolism of dietary fats, proteins, and carbohydrates	Fatigue, loss of appetite, nausea, vomiting, depression, muscle pains, weak finger and toenails, alopecia, heart abnormalities and anaemia	Liver, kidney, egg yolk, milk, most fresh vegetables, yeast bread and cereals	30 μg/day (adults, and pregnancy), 35 μg/day (lactation)	(Osuagwu, 2019; Yang et al., 2023)
Folate (vitamin B9)	Promotion of red blood cell formation and lowering the risk of neural tube birth defects and coronary heart disease, liver damage repair, cell division, protein metabolism, tissue buildup, muscle protection, and growth	Overall growth impairment. Megaloblastic anaemia, heart disease, stroke, and an increased risk of certain types of cancer are also symptoms of deficiency. Deficiency in pregnant or child-bearing women may result in the birth of a baby with neural tube defects such as spina bifida	Liver, kidney, dark green leafy vegetables, mushrooms, meats, fish, whole grains, fortified grains and cereals, legumes, citrus fruits and African fermented foods such as *ogi*, *mahewu*, *ben-saalga* and *ogiri*	400 μg/day (adults), 600 μg/day (pregnancy), 500 μg/day (lactation)	(Celep et al., 2017; Ndiaye, Idohou-Dossou, Diouf, Guiro, & Wade, 2018; Obafemi et al., 2022; Said, 2014)
Cobalamin (vitamin B12)	Contribution to the formation of genetic material, production of normal red blood cells, and maintenance of the nervous system	Megaloblastic anaemia (associated with *Helicobacter pylori*-induced gastric atrophy), neurological disorders, growth retardation, and nerve degeneration resulting in numbness and tingling	Meats, liver, kidney, fish, eggs, milk and milk products such as nono, oysters, and shellfish	2.0 μg/day (adults), 2.6 μg/day (pregnancy), 2.8 μg/day (lactation)	(Celep et al., 2017; Gebremedhin, 2021; Green et al., 2017; Mikkelsen & Apostolopoulos, 2019)

[a] Recommended Dietary Allowance.

Table 2
Prevalence (%) of B-group vitamin deficiencies in different African countries.

Vitamin	Affected population	Region/country in Africa	Prevalence (%)	Year	Reference
Thiamin (vitamin B1)	Adults	Guinea	41.9	2015	Whitfield et al. (2018)
	Men (29 years mean)	Somalia	23.3	2009/2010	Watson et al. (2011)
	Adults	Cote d'Ivoire	64	2008	Aké-Tano et al. (2011)
Riboflavin (vitamin B2)	Children under 5	Cote d'Ivoire	65	2004/2005	Rohner et al. (2007)
		Uganda	49.6	2009	Nichols et al. (2013)
Niacin (vitamin B3)	Children under 5	South Africa	6	2013	Seal et al. (2007)
	Women of reproductive age (15–49)		29.4		
Pantothenic acid (vitamin B5)	Pregnant women (15–40)	Nigeria	0	2021	(Umar et al., 2022)
Pyridoxine (vitamin B6)	N/A	N/A	N/A	N/A	
Biotin (vitamin B7)	N/A	N/A	N/A	N/A	
Folate (vitamin B9)	Children under 5	Cameroon	18	2009	Stevens et al. (2022)
	Women of reproductive age (15–49)	Cameroon	35	2009	Stevens et al. (2022)
		Cote d'Ivoire	91	2007	
		Ethiopia	32	2015	
		Ghana	59	2017	
Cobalamin (vitamin B12)	Pregnant women	Middle East and North Africa	30.76	2017	Ritchie and Roser (2017)
		Sub-saharan Africa	45.83	2017	Ritchie and Roser (2017)
		Middle East and North Africa	30.32	2017	
		Sub-saharan Africa	40.55	2017	
	Women of reproductive age (15–49)	Malawi	54	2018	Gebremedhin (2021)
		Kenya	34	2018	
		Ethiopia	15	2018	
		Ghana	7	2018	
	Children under 5	Middle East and North Africa	33.63	2017	Ritchie and Roser (2017)
		Sub-saharan Africa	60.49	2017	

N/A – Not available.

2017). Indeed, according to the Food and Agriculture Organization of the United Nations (FAO), in 2018, the meat supply in many African countries was below 20 kg/person/year, while the average milk consumption was less than 50 kg/person/year (Ritchie, Rosado, & Roser, 2017). Animal-based foods provide several vitamins and are the only source of cobalamin. However, plant-based foods are also important sources of B-vitamins, such as folate and thiamin, but their consumption is also often limited. Undoubtedly, there are concrete constraints to store perishable raw matrices ensuring an adequate control of the cold chain, while food-processing industry is lacking in rural area. On the other hand, food processing leads to losses of water-soluble and thermally labile vitamins. However, a limited dietary diversification is only partially explained by the general poverty and the low industrialization rate of several African countries. Seasonal variation can strongly impact on malnutrition, making staple foods only available in some periods of the year. In rural area of sub-Saharan Africa, most households are subjected to a prolonged dry season, thus towards the end of the dry season (the so-named 'hunger period') perishable foods are limited (de Jager, van de Ven, Giller, & Brouwer, 2023; Waswa, Jordan, Krawinkel, & Keding, 2021).

Moreover, ethnic groups can promote different traditional food cultures and patterns. For example, some religions and/or taboos encourages the consumption of meat products only by men, thus reducing the diversity of diets of women and children (Oniang'o, Mutuku, & Malaba, 2003). Furthermore, other socio-economic factors including the educational level of the mother has been reported to impact on the likelihood of children to suffer malnutrition (Fongar, Linderhof, Ekesa, Dijkxhoorn, & Nalweyiso, 2023; Khulu, Ramroop, & Habyarimana, 2023).

In terms of policy interventions, efforts to intensify promotion of crop diversification are considered a priority to contrast malnutrition threat in Malawi (Kerr et al., 2019; Mango, Makate, Mapemba, & Sopo, 2018). Moreover, the burden of climate change should support the cultivation of "forgotten" food crops such as leafy vegetables, fruits, cereals, pulses, seeds and nuts, roots and tubers, as a strategy to complement micronutrient provision (van Zonneveld et al., 2023). Finally, investing in the development of accessible market also by improving rural infrastructure is essential to ameliorate household dietary diversity (Usman & Haile, 2022).

3.2. *Supplementation*

Supplementation is defined as the provision of a single or multiple micronutrients in the form of capsules, tablets, drops or syrup (Tam, Keats, Rind, Das, & Bhutta, 2020). Supplementation is one of the most common active intervention strategies and has been confirmed to be efficacious in controlling the effect of micronutrient malnutrition and, ultimately, hindering chronic health conditions in developed countries (Bánhidy, Ács, Puhó, & Czeizel, 2011; Islam et al., 2016). Some examples of supplements include United Nations International Multiple Micronutrient Antenatal Preparation (UNIMMAP) developed by United Nations Children Funds (UNICEF), the United Nations University, and WHO (Devakumar et al., 2016). However, the cost of production of these products is high and is not readily available and affordable in most African countries.

3.3. *Fortification*

Fortification is defined as the deliberate addition of one or more micronutrients (i.e. vitamins and minerals) to improve the nutritional value of some foodstuffs. Food fortification can be mandatory when governments oblige to fortify specific foods with specified micronutrients, or on voluntary base when producers freely choose to fortify particular foods. In general, mandatory fortification are applied on large-scale to contrast widespread events of malnutrition among the population and mainly refers to micronutrients such as iodine, iron, vitamin A and folic acid. In South Africa, mandatory fortification of cereal staple foods was implemented in 2003 as part of the National Food Fortification Programme. The adoption of these preventive measures revealed a significant increase of the intake of vitamin A, thiamin, niacin, pyridoxine, folic acid and iron in 1- to 9-year-old children (Steyn, Nel, & Labadarios, 2008). Similarly, a recent survey on a cohort of 12-months-old children showed that the consumption of fortified porridge in South Africa linked to an adequate intakes for all eight fortificant nutrients including, thiamin, niacin, pyridoxine and folate for more than 50% consumers (Swanepoel et al., 2019). Nonetheless, mandatory programs should take in account the risk of over-supplementation, as reported for hypervitaminosis A in Zambia and South Africa (Tanumihardjo, Kaliwile, Boy, Dhansay, & van

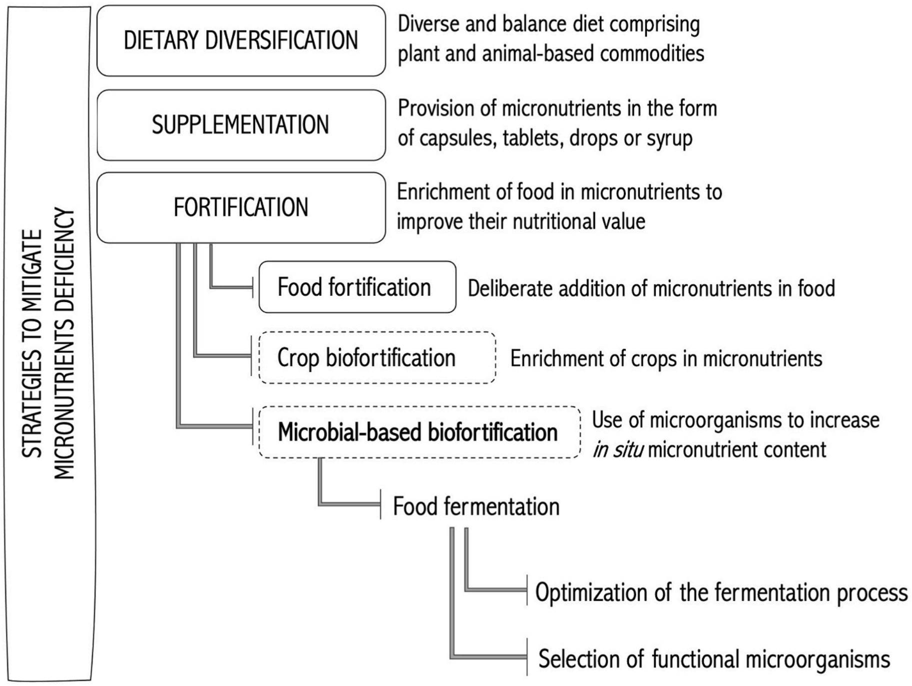

Fig. 1. Food-based strategies to mitigate micronutrient deficiency. For each approach, the definition is given. With dashed line, the biotechnological approaches are indicated. In bold, the core topic covered in this review paper.

Stuijvenberg, 2019). However, this eventuality is rather low for B-group vitamins, which, being water-soluble, are not accumulated in the body.

In contrast, crop biofortification aims to obtain crops enriched in vitamins and minerals through plant breeding, bioengineering techniques, or agronomic practices. These biotechnological solutions have been mainly applied to staple foods, such as maize and beans, to increase the level of provitamin A, selenium, iron, and zinc (Galani et al., 2022; Huertas et al., 2023). However, it is noteworthy that to the best of our knowledge, no crops have been biofortified with vitamins of the B-group in Africa. Therefore, further research should be performed to evaluate the effectiveness of biofortification strategies, the acceptability of these products by consumers in African countries (Siwela et al., 2020), as well as the possibility to extend these approaches also to the B-group vitamins.

Lastly, another promising approach that can be implemented to increase B-group vitamins in food is the microbial-based biofortification, i.e. the use of selected microorganisms to increase *in situ* the content of vitamins during food fermentation. It is important to emphasize that this is a general strategy that may be applied to fermented foods from different sources and not limited to crops. Moreover we focus here on the employment of food-grade not-genetically modified bacteria that can be deliberately added into the food chain. On the contrary, metabolic engineering approaches have been proposed, for the biotechnological production of riboflavin, folate and cobalamin (Nguyen-Vo et al., 2018; Revuelta et al., 2018; You et al., 2021) but their employment could be submitted to regulatory restriction among different countries. In this review, we mainly focus on plant-based fermented food from Africa and report some strategies that can be implemented to increase the B-group vitamins content of such food namely i) the optimization of the fermentation process and ii) the selection of functional microorganisms (Fig. 1).

4. Plant-based African fermented foods as natural sources of B-group vitamins

Fermentation is an ancestral biotechnology process to increase safety, shelf life, as well the nutritional value of perishable raw matrices due to the microbial metabolism (Diez-Ozaeta & Astiazaran, 2022). Yeasts and lactic acid bacteria (LAB), respectively, through alcoholic and lactic fermentation, contribute to the production of most fermented foods. On the other hand, alkaline fermentation of high-proteins raw matrices, mainly carried out by some *Bacillus* spp., it is a process to obtain various traditional African foodstuffs (Owusu-Kwarteng, Parkouda, Adewumi, Ouoba, & Jespersen, 2022). The biochemical transformations that occur during fermentation can make the final product more nutritious (e.g. increasing the vitamin content), more digestible (e.g. reducing the levels of antinutritional compounds such as tannins, phytates, and trypsin inhibitors that limit the digestibility and bioavailability of essential nutrients), safer (e.g. inhibiting foodborne pathogens) or tastier (e.g. increasing flavor compounds) (Obafemi et al., 2022). The ability to synthesize B-group vitamins is widely reported among different microorganisms (both yeasts and bacteria) that are usually involved in food fermentation. This feature seems to be strain-dependent and probably evolved depending on the availability of these micronutrients in the environment. During spontaneous fermentation, indigenous microorganisms are responsible for the fermentation process, and they could increase the vitamin content.

In particular, plant-based fermented food typically consumed in African countries can be classified as (i) fermented tubers; (ii) fermented cereal products; (iii) fermented legumes and (iv) fermented leafy vegetables, and some of them have been reported to be a source of B-vitamins, as summarized in Table 3.

4.1. Fermented tubers

Cassava (*Manihot esculenta* Crantz) and yam (*Dioscorea alata*) are examples of root crops, and they are among the most abundant starch food in African countries. During processing, the tubers are usually peeled, washed, milled and fermented either by solid-state and submerged fermentation process for 3–5 days and then granulated into different fermented products, which include *gari*, *fufu*, *lafun* or *kokonte* in Nigeria and Ghana; *agbelima* a Ghanaian cassava dough; and *attieke* (Elegbeleye et al., 2022). Although cassava is highly rich in vitamin A (0.92 μg/g) and vitamin C (23.27 mg/g) (Airaodion, Airaodion, Ewa, Ogbuagu, & Ogbuagu, 2019), little research has been reported on B-group vitamins contents. Specifically, cassava roots are reported to contain low amounts of riboflavin, niacin, and thiamin (0.048, 0.854 and 0.087 mg/100 g, respectively) (Bayata, 2019; Montagnac, Davis, & Tanumihardjo, 2009).

4.2. Fermented cereal products

Cereal-based products constitute an important group of substrates for fermented foods in Africa. Fermented porridges and beverages are mostly used as essential functional foods for children and as part of infant weaning diets. Staple foods from maize or corn (*Zea mays*), sorghum (*Sorghum bicolor*), millet (*Pennisetum glaucum*) or wheat (*Triticum aestivum*) undergo nutritional and biochemical changes during fermentation (Embashu & Nantanga, 2019; Oyeyinka, Siwela, & Pillay, 2021). The cereal-based fermented products can be in the form of a paste or a slurry as in the case of *ogi* (Nigeria), *akasa* (Ghana), *uji* (Kenya), *abreh* (Sudan), *mahewu* (Zimbabwe and South Africa), including fermented drinks like *burukutu* and *kunnu* (Nigeria) (Ezekiel et al., 2018; Obinna-Echem, 2017; Adebo, 2020; Mashau et al., 2021).

In general, African cereal-based fermented foods are a good source of B-group vitamins-producing microorganisms, as corroborated by genetic screening that revealed the occurrence of pathways for folate and riboflavin synthesis (Humblot & Guyot, 2009; Turpin, Humblot, & Guyot, 2011). Although the functionality of the corresponding operons should be further investigated, omics approaches can provide interesting preliminary information on the frequency of microbial vitamin biosynthesis in complex food ecosystems. For example, the high rate of genes *folP* and *folK*, and the low frequency of detection of the gene *ribG* indicate that LAB in *ben-saalga* have a different genetic potential to synthesize folate and riboflavin, respectively (Saubade, Humblot, Hemery, & Guyot, 2017).

It has been reported that B-group vitamin content rise during the natural fermentation of cereals, although considerable dissimilarities were found in different reports (Achi & Asamudo, 2019; Bationo et al., 2020). Compared to the raw matrix, *munkoyo* a fermented maize-product was found to be a source of B-vitamins, whose levels of vitamin B1, vitamin B3 and vitamin B6 were similar to those in *mabisi*, a milk-based fermented food (Chileshe, van den Heuvel, et al., 2020). However, a recent study, supported by the employment of Optifood modelling, indicated that the inclusion of *Mabisi* (and not *munkoyo*) can have a major impact on the nutrient adequacy (Chileshe, Talsma, et al., 2020). Changes in B-group vitamins during spontaneous fermentation of cereals are influenced by several factors, such as the raw matrix, condition of fermentation and microorganisms involved (Bationo et al., 2020; Chaves-López, Rossi, Maggio, Paparella, & Serio, 2020; Saubade, Hemery, Rochette, Guyot, & Humblot, 2018). Folate, thiamine, riboflavin and niacin content of the most common fermented cereal gruel in West Africa is 0.031 0.75, 0.37 and 2.21 mg/100 g, respectively (Greppi et al., 2017; Okoroafor, Banwo, Olanbiwoninu, & Odunfa, 2019; Rouf Shah, Prasad, & Kumar, 2016). Recently, it has been reported that during *ogi* production the simultaneous fermentation of cereals and underutilized edible plants, like tigernut and sesame, increased the level of niacin, thus counteracting the significant losses of essential nutrients as consequence of processing cereal grains into slurries (Banwo et al., 2022).

4.3. Fermented legumes

The use of fermented legumes in seasoning has long been in practice in Africa, and widely recognized (Olanbiwoninu & Odunfa, 2018; Olasupo, Okorie, & Oguntoyinbo, 2016). In Africa, many protein-rich seeds are fermented to make food condiments including *iru* or *dawadawa*, *tempeh*, *soumbala*, and *netetu* from African locust beans (*Parkia biglobosa*) (Nigeria, Ghana, Burkina Faso, Senegal), *ugba* from African oil beans *Pentaclethra macrophylla* (Nigeria, Benin), *ogiri* from either castor oil beans or melon seeds (*Ricinus communis or Citrullus vulgaris*) (Nigeria), *okpehe* from prosopis Africana seeds (*Prosopis africana*) *owoh* from African yam beans (*Sphenostylis stenocarpa*) (Nigeria) and *siljo* from faba beans flour (*Vicia faba*) in combination of with safflower (*Carthamus tinctorius*) (Ethiopia) (Chinma et al., 2020; Esse et al., 2022). Several reports confirmed that the levels of B-group vitamins can be higher in fermented legumes than in the raw materials, especially for riboflavin (0.0084–0.0261 mg/100 g), thiamine (0.0018–0.0023 mg/100 g), niacin (0.0031–0.0033 mg/100 g) and folate (0.03 mg/100 g) (Olanbiwoninu, Irokosu, & Odunfa, 2017; Olasupo, 2005; Termote et al., 2022). Interestingly, fermentation of African yam bean yoghurt-like determined a critical reduction (75%) of riboflavin while thiamine increase of about 20% (Aminigo, Metzger, & Lehtola, 2009).

4.4. Fermented leafy vegetables

African indigenous leafy vegetables are characterized by high nutritional potential and represent an underexploited source of micronutrients. In the last years, spontaneous fermentation of these matrices has been proposed as a tool to modulate the phyllosphere microbiota in order to ensure a more stable product with enhanced nutritional quality (Misci, Taskin, Vaccari, Dall'Asta, et al., 2022a, 2022b). In particular, pumpkin leaves submitted to submerged fermentation showed a significant increase in pyridoxine and folate; folate content being three-folds higher than in the corresponding raw material. Interestingly, the proposed approach allowed to achieve a concentration of folate of 270 μg/100 g, a level exceeding the dietary reference value (250 μg per day for adults) (Misci et al., 2021). Processing in a similar way amaranth leaves, typically consumed in sub-Saharan Africa, it was observed that fermentation increased the concentration of thiamin, riboflavin, and pyridoxine, while reduced pantothenic acid and niacin (Misci, Taskin, Vaccari, Dall'Asta, et al., 2022b).

5. Impact of food processing and fermentation conditions on B-group vitamins content

Vitamins are reactive compounds whose retention can be influenced by various factors during processing and storage, including, among others, pH, heat, and exposure to light (Bui, Small, & Coad, 2013). As mentioned above, cereal-based fermented foods are largely consumed in African countries and are an important source of micronutrients and, in particular, of B-group vitamins (Capozzi, Russo, Dueñas, López, & Spano, 2012). However, cereal grains are submitted to different processes, including debranning, soaking, wet-milling, heating, fractionation, cooking, and storage, that can result in a reduction of the vitamin content due to the physical removal of grain fractions, as well as to the loss of thermolabile, water-soluble and photosensitive compounds (Saubade, Hemery, et al., 2017). A recent study reported the impact of processing on the folate content of traditional cereal-based fermented foods consumed in West African countries (i.e. *akassa*, *doncounou*, *kaffa*, *fura*, *massa*, *ben-kida*, and *ben-saalga*) indicating that porridge and gelatinized products showed different loss of this vitamin (Bationo et al., 2020). Thus, though genes for the synthesis of folate were abundant in *ben-saalga*, a typical porridge consumed in Burkina Faso, its folate content was rather low, suggesting that this vitamin diminished during food processing (Saubade et al., 2018). Accordingly, two thermal treatments (i.e. air-drying or boiling) employed to stabilize fermented amaranth leaves have a different impact on the level of B-group vitamins (Misci et al., 2022b), while niacin was negatively affected by submerged fermentation of pumpkin leaves (Misci et al., 2021). Similarly, African kale leaves submitted to submerged fermentation by using selected LAB strains strongly decreased the levels of thiamin and riboflavin (i.e. more than 70%, and about 60%, respectively), that was partially explained by their loss into the watery phase (Oguntoyinbo et al., 2016). Consequently, an increased knowledge of the critical steps reducing the vitamin content should allow to implement technological modifications

Table 3
Occurrence of B-group vitamins in African fermented plant-based foods and microorganisms involved in the fermentation processes.

Fermented foods	Country	Raw material	Form of consumption	B-group vitamins	Concentration (mg/100 g)	Estimated daily consumption of vitamin/ %RDA mg/day[a]	Main microorganisms involved	References
Tubers								
Garri	Nigeria	Cassava pulp	Soaked garri (in water) *Eba or Amala* (cooked into a dough with hot water) eaten with soup	B1 B2 B3	0.087 0.0048 0.854	0.26/19.96 0.014/1.1 2.55/16.22	*Leuc. Mesenteroides* *L. plantarum* *Streptococcus* spp. *Geotricum candidum*	(Adowei, Ebenezer, & Markmanuel, 2020; Bayata, 2019)
Attieke	Côte d'Ivoire	Cassava pulp	Couscous	N/A	N/A	N/A	*Bacillus subtilis*	
Lafun	Nigeria/ Ghana	Cassava pulp	*Amala*	N/A	N/A	N/A		
Fufu	Nigeria	Cassava pulp	Dumpling	N/A	N/A	N/A		
Cereal grains								
Ogi	West Africa	Maize, sorghum millet	Porridge	B1 B2 B3 B9	0.75 0.37 2.21 0.031	0.43/33.31 0.21/16.44 1.28/8.13 0.018/3.74	*Lactobacillus* spp. *Corynebacterium* spp. *Acetobacter* spp. *Streptococcus lactis*	(Bationo et al., 2020; Ezekiel et al., 2018; Okoroafor et al., 2019; Okafor, Omemu, Obadina, Bankole, & Adeyeye, 2018; Saubade et al., 2018; Obinna-Echem, 2017; Saubade, Hemery, Guyot, & Humblot, 2017)
Akasa/koko	Ghana		Porridge	N/A	N/A	N/A	*Saccharomyces cerevisae*	
Uji	Kenya		Porridge	N/A	N/A	N/A	*Rodotorula* spp.	
Mahewu	South Africa		Non-alcoholic beverage	N/A	N/A	N/A	*Candida mycoderma*	
Abreh	Sudan		Porridge	N/A	N/A	N/A	*Debaryomyceshansenii*	
Kunun-zakii	Nigeria		Non-alcoholic beverage	N/A	N/A	N/A	*Weissella* spp.	
Ben-saalga	Burkina Faso		Porridge/gruel	B9	0.0022	N/A	*Leuconostoc* spp.	
Mawe	Benin		Gruel	N/A	N/A	N/A	*Pediococcus* spp.	
Legumes								
Iru/ Dawadawa	Nigeria	African locust bean Soybean	Condiment	B1 B2 B3 B9	0.0023 0.0261 0.0033 0.03	0.00023/0.02 0.00021/0.2 0.00033/0.002 0.003/0.63	*B. subtilis* *Bacillus licheniformis* *Staphylococcus* spp.	(Kustyawati et al., 2020; Olanbiwoninu et al., 2017; Ouoba, 2017; Romulo & Surya, 2021)
Soumbala	Burkina Faso		Condiment	N/A	N/A	N/A		
Netetu	Senegal		Condiment	N/A	N/A	N/A		
Kinda	Sierra Leone		Condiment	N/A	N/A	N/A		
Afitin	Benin		Condiment	N/A	N/A	N/A		
Tempeh	Ghana	Soy bean	Cake/meat sustitute	N/A	N/A	N/A	*Rhizopus* spp.	
Ogiri	Nigeria	Melon seed Fluted pumpkin Castor oil seed	Condiment	B1 B2 B3 B6 B9	0.75 0.01 38.60 0.10 60.80	0.075/5.76 0.001/0.08 3.86/22.79 0.010/0.56 August 6, 1266.5	*Bacillus* spp. *Escherichia* spp. *Pediococcus* spp.	(Arukwe & Onyeneke, 2020; Oguntoyinbo, 2014)
Ugba	Nigeria	African oil bean	Condiment	B1 B2 B3	0.07 0.30 0.30	0007/0.47 0.03/2.01 0.03/0.19	*B. licheniformis* *Micrococcus* spp. *Staphylococcus* spp.	Anyanwu, Okonkwo, Iheanacho, and Ajide (2016)
Palmwine	West Africa	Palm sap	Alcoholic beverage	B3	14.86	N/A	*Saccharomyces* spp. Lactic acid bacteria Acetic acid bacteria	Hebbar et al. (2018)

N/A – Not available.

[a] Estimated daily consumption of vitamin is calculated based on the estimated daily intake of each fermented food using the formula: $\frac{Concentration\ of\ B - vitamin\ in\ food\ (mg)}{weight\ of\ food\ quantified\ (g)}$ * Estimated daily consumption of food (g) e.g the estimated daily intake of *garri* is 299 g. Hence, the estimated daily consumption of vitamin B1 in *garri* = 0.087/100*299. The % RDA (mg/day) = $\frac{\text{estimated daily consumption of vitamin}}{\text{Average RDA of vitamin}}$ * 100.

to encourage their retention. For example, the suppression of the sieving step and the use of whole flour has been proposed to enhance the folate content of *ben saalga* (Saubade et al., 2018), while optimizing heating conditions, including type of heating, duration, and temperature, in particular for cereals-based fermented foods, might limit vitamin B losses as recently reviewed (Padonou, Houngbédji, Hounhouigan, Chadare, & Hounhouigan, 2023).

On the other hand, the optimization of some conditions of the fermentation process could also impact on the vitamin content. For instance, increasing the fermentation time during bread-making to up to 16 h allowed to obtain a bread with a content of riboflavin about three-fold higher compared to a 4-h fermentation step (Russo, Capozzi, et al., 2014a). Interestingly, this approach is more suitable in a framework such as that of the African rural area, mainly characterized by traditional and home-made fermented foods, rather than for industrial productions since increasing the production time implies higher costs. However, these solutions are often difficult to apply due to consolidated eating and cultural habits that take time to be modified.

6. Microbial-based biofortification to enhance B-group vitamins content of plant-based African fermented foods

As reported above, plant-based African fermented foods are good sources of B-group vitamins, whose content can be enhanced by optimizing some conditions of fermentation and/or processing. However, even if the fermentation process can impact to a different extent on the concentration of B-group vitamins mainly due to the *in situ* microbial production, further research is needed to evaluate cross-feeding interactions during fermentation between producers and non-producers microorganisms and the actual impact on food vitamin content. Indeed, depletion by auxotrophic indigenous microorganisms could also have a detrimental effect on the level of some vitamins (Kariluoto et al., 2006). Therefore, microbial-based approaches, including a targeted selection as well a proper management of the microbial resources employed, can be implemented to increase the level of these vitamins during fermentation. In particular, the selection of functional microbial strains able to produce higher levels of specific vitamins is pivotal for their *in situ* vitamin production during food fermentation, also known as microbial-based biofortification. The functional microorganisms can be mainly select based on (i) which B vitamin they produce, (ii) which vitamin vitamer they produce and whether the production is intracellular or extracellular.

6.1. Selection of microorganisms based on B-group vitamin production

6.1.1. Selection of food-grade folate producing strains

In the last years, several studies have been performed to select microorganisms producing high levels of folate, riboflavin, cobalamin, and thiamine from traditional fermented foods (Carrizo et al., 2017; Jiménez et al., 2018; Teran, de Moreno de LeBlanc, Savoy de Giori, & LeBlanc, 2021). However, to the best of our knowledge, screening of a large cohort of indigenous food-grade microbes from ethnic African foods have been mainly focused on the selection of folate-producing strains. In a recent study, 220 presumptive LAB isolated from maize gruel were screened for their folate production, and the best candidates were employed as starters to obtain sorghum *motoho* with a final amount of folate up to eight times higher than the control (about 20 μg/100 mL), a level adequate to cover young children's daily folate requirements (Fayemi, Akanni, Sobowale, Oelofse, & Buys, 2023). Similarly, high-folate-producing strains belonging to the *Lactiplantibacillus plantarum* species were selected among 162 presumptive LAB isolated from *injera*, a fermented flat bread widely consumed in Ethiopia (Tamene et al., 2019). The best strain was used in mixed fermentation with a commercial *Saccharomyces cerevisiae* to prepare *injera* by simulating a traditional backslopping process achieving a concentration of 53.5 μg/100 g fresh material. These results provide encouraging indications about the elaboration of home-made local foods covering up to 22% of the recommended nutrient intakes of folate (Tamene, Baye, & Humblot, 2022). Cereal-based fermentation involves the contribution of both yeast and bacterial communities. However, even if yeasts can synthesize some B-group vitamins, including folate, few studies have been focused on their selection based on the optimization of this feature. Recently, a strain of *Pichia kudriavzevii* selected among 93 autochthonous yeast isolates was proposed in co-fermentation with *Limosilactobacillus fermentum* in a model of fermented pearl millet-based gruel to enhance the folate content until 4 μg/100 g fresh matter (Greppi et al., 2017). Interestingly, the same yeast species (previously known as *Candida krusei*) was highly prevalent in traditional West African products (Greppi, Rantisou et al., 2013a, 2013b), and it was characterized for its probiotic aptitudes, thus emphasizing the hypothesis that folate could be synthesized *in situ* in the gut environment (Greppi et al., 2017). Accordingly, B-group vitamin-producing probiotic bacteria are considered an attractive solution to reduce avitaminosis (as reviewed by LeBlanc et al., 2017). Interestingly, the most productive folate-producing *L. plantarum* strain isolated from *injera* was able to revert folate deficiency in a murine model suggesting alternative solutions than consuming folate-rich foods to mitigate the lack of this vitamin (Tamene et al., 2019).

6.1.2. Selection of food-grade riboflavin-overproducing strains

It is important to point out that under physiological conditions, the microbial production of vitamins is low and inconsistent with the *in situ* biofortification concept. Only seldom spontaneous overproducing strains have been isolated, as is the case of a vaginal isolate of *Limosilactobacillus reuteri* (Spacova et al., 2022). This strain showing the higher riboflavin production (more than 18 μg/mL) reported until now within LAB, was employed as a promising starter for the riboflavin *in situ* biofortification of plant-based and dairy fermented foods. Moreover, the ability to survive in a model mimicking the gastrointestinal environment, the passive transport of riboflavin in the small intestinal and colon, and its active transport via intestinal epithelial Caco-2 monolayers strongly suggested that this strain might play a beneficial role in the human gastrointestinal tract (Spacova et al., 2022). In the past years, exposure to the selective pressure of roseoflavin, a toxic analogous of riboflavin, has been reported as a biotechnological strategy to select spontaneous riboflavin-overproducing derivative LAB strains (Burgess, O'connell-Motherway, Sybesma, Hugenholtz, & van Sinderen, 2004; Russo et al., 2021). In particular, mutations occurring in the riboswitch regulatory region of the *rib* operon decreased the stability of the aptamer even in the presence of the effector, thus promoting its impaired regulation (Ripa et al., 2022). In this way, food-grade derivative spontaneous mutants were able to produce higher levels of riboflavin than the corresponding parental strains. In the last years, several strains belonging to the species *Lactiplantibacillus plantarum*, *Limosilactobacillus fermentum*, *Leuconostoc mesenteroides*, *Lactococcus lactis*, *Weissella cibaria* and *Propionibacterium freudenreichii* have been isolated from different food matrices and selected after exposure to roseoflavin (Burgess, Smid, Rutten, & van Sinderen, 2006; Capozzi et al., 2011; Hernández-Alcántara et al., 2022; Russo, Capozzi, et al., 2014a, 2014b; Yépez et al., 2019). These strains have been employed to elaborate riboflavin-enriched fermented foods such as yoghurt, bread, and pasta (Burgess et al., 2006; Capozzi et al., 2011; Hernández-Alcántara et al., 2022; Russo, Capozzi, et al., 2014a, 2014b). On the other hand, some riboflavin -overproducing LAB strains have been submitted to a comprehensive probiotic characterization using both *in vitro* and *in vivo* models (Arena et al., 2014; Mohedano et al., 2019; Russo, Iturria, et al., 2015a, 2015b), resulting in suitable solutions for the production of functional biofortified foods such as oat-based beverages (Russo et al., 2016), cereal-based kefir-like (Yépez et al., 2019), soy milk (Zhu et al., 2020), and okara (Wang, Xie, et al., 2022a). Moreover, fresh-cut fruits, namely pineapples and cantaloupe, have also been reported as innovative carriers to vehicle beneficial probiotic riboflavin-overproducing strains (Russo, de Chiara., 2014b; Russo, Peña, et al., 2015b). To the best of our knowledge, no study report on the selection of roseoflavin-resistant spontaneous riboflavin-overproducing LAB strains isolated from fermented African products. However, the species until now reported as riboflavin-overproducing are typical inhabitants of plant-based African matrices during spontaneous fermentation (Adepehin, 2020), making it a promising field for future researches. For example, selected strains of *L. plantarum* and *L. fermentum* have been recently employed as starters to produce *ting*, a traditional fermented sorghum product mostly eaten in Southern Africa (Kewuyemi et al., 2020) and African nightshade leaves (Stoll et al., 2021).

6.1.3. Selection of food-grade cobalamin producing strains

Unlike other B-group vitamins, only few LAB strains are known to encode complete *de novo* biosynthetic pathways of cobalamin, including *L. reuteri* (Taranto, Vera, Hugenholtz, De Valdez, & Sesma, 2003), *L. fermentum* (Basavanna & Prapulla, 2013), *Furfurilactobacillus rossiae* (De Angelis et al., 2014), *Loigolactobacillus coryniformis* (Torres et al., 2016), and *L. plantarum* (Bhushan, Tomar, & Mandal, 2016). Although most of these LAB species are ubiquitous and typical inhabitants of different edible raw matrices, only limited results have been reported about the *in situ* cobalamin enrichment of fermented soy-milk products (Bhushan et al., 2016; Gu, Zhang, Song, Li, & Zhu, 2015). However, cobalamin production by LAB is under dispute for their ability to synthesize corrinoid compounds (also known as pseudovitamins) different than active cobalamin, which at intestinal level have a lower affinity for transporters, making it unavailable to humans (Varmanen, Deptula, Chamlagain, & Piironen, 2016). To date, different biosynthetic pathways of cobalamin-type corrinoid compounds have been described in LAB (Torres, Vannini, Font, Saavedra, & Taranto, 2018), and the occurrence of purine intermediate has been reported to shift the production of cobalamin, instead of pseudo-cobalamin (Torres, Elean, Hebert, Saavedra, & Taranto, 2020). However, microbiological or immunoassays, that are widely used to perform large screening, cannot differentiate between active forms and pseudovitamins, thus often leading to an overestimation of its production.

On the other hand, cobalamin synthesis by propionic acid bacteria is well known. *Propionibacterium* spp. Is mainly associated with dairy and fermented dairy products (Moslemi, Mazaheri Nezhad Fard, Hosseini, Homayouni-Rad, & Mortazavian, 2016). Traditional fermented dairy products in Africa include *nono* (Nigeria, Ghana), *wara* (Nigeria, Togo), *fene* (Côte d'Ivoire, Mali), *suusac* (Kenya, Somalia), *pendidam* (Cameroon), *gariss* (Sudan), *nyamie* (Ghana), *leben/lben* (Tunisia) and *kulenaoto* (Kenya) that are considered good sources of cobalamin (Gille & Schmid, 2015). Although, Africa features a unique richness of milk-based fermented products (Jans et al., 2017), in general, dairy products are consumed in low amounts mainly due to the seasonality of the milk, the difficulty of a correct management of the cold chain, and why producers use milk as a source of income rather than for consumption (Agyei, Owusu-Kwarteng, Akabanda, & Akomea-Frempong, 2020). Therefore, plant-based alternatives to yoghurt have been proposed as source of essential nutrients and bioactive compounds using locally available ingredients in East Africa (Dusabe, Chacha, Vianney, & Raymond, 2022).

Interestingly, recently, *Propionibacterium freudenreichii* has been tested in mixed fermentation with LAB by using cereals (i.e. wheat, oat, rice, and rye bran, as well millet and sorghum flours), pseudocereals (i.e. buckwheat bran, amaranth and quinoa flours), and legumes (i.e. soybean, faba bean, and lupine flours) as promising substrates for cobalamin fortification (Wang, Xie, et al., 2022a, 2022b; Xie et al., 2018, 2021). In a recent study, *Propionibacterium* spp. Has been found during the processing of different formulations of *kunu*, a traditional cereal-based fermented beverage (Ezekiel et al., 2018), strongly suggesting that selected *Propionibacterium* spp. strains could be used to design starter cultures for the fermentation of a wide variety of African cereal-based products.

Therefore, further exploiting the technological performances of *Propionibacterium* spp. could be a suitable and low-cost solution to apply for some cereal-based fermentation, as well non-dairy yogurt-like in order to obtain cobalamin-enriched fermented African foods.

6.2. Selection of microorganism based on the vitamers produced and on the intra/extracellular production

Another critical point to consider for the purpose of increasing B-group vitamins via microbial-based approaches is the vitamin vitamers i. e. the closely related forms of the same vitamins, characterized by different physiological activities and metabolism, as well bioavailability and abundance in foods (Jakobsen, Melse-Boonstra, & Rychlik, 2019). Several conditions occurring during fermentation and/or processing might contribute to the degradation and/or interconversion of vitamers with different stability. In particular, many folate vitamers are pH-sensitive whereas folic acid is stable under neutral and alkaline conditions. On the other hand, tetrahydrofolate , the main vitamer in some pulses, is unstable at high temperatures, thus resulting in major losses during cooking (Saubade, Hemery, et al., 2017). Moreover, tetrahydrofolate was lost during digestion simulation, and the structure of the food matrix has been reported to play a key role protecting sensitive folate vitamers during the gastric phase, thus increasing its bioaccessibility (Bationo et al., 2020; Ringling & Rychlik, 2017).

These evidences suggest that the selection of starter cultures mainly producing vitamers that are functional in acidic environments and/or more stable to heat treatments could be a useful strategy to enhance the folate content of some fermented foods and that food matrices could be modified to increase their bioavailability for humans (Liu, Edelmann, Piironen, & Kariluoto, 2022).

Similarly, the selection of strains able to produce higher levels of extracellular rather than intracellular vitamins is another factor increasing the bioavailability, as reported for folate (Fayemi et al., 2023), riboflavin (Ripa et al., 2022), and cobalamin (Li, Gu, Yang, Yu, & Wang, 2017). Interestingly, a long-time fermentation of pearl millet was associated to an increase of folate probably due to cell autolysis in stationary phase and the release of bioaccessible vitamin (Greppi et al., 2017).

7. Conclusions

Micronutrient deficiency is a common condition shared among developing and low- and middle-income African countries. In particular, the insufficient intake of vitamins of the B-group has received less attention compared to other micronutrients such as vitamins A and D, iron, and zinc. Although traditional plant-based African fermented foods are important sources of B-vitamins, some microbial-based approaches might be useful to enhance their content. In particular, the selection of pro-technological functional microbial strains from spontaneous fermentation and/or unconventional food matrices, as well as the implementation of adequate food processing techniques, are promising tools to improve the amount and bioavailability of B-vitamins. On the other hand, an effort should be recommended to develop accessible guidelines about controlling and monitoring of fermentation in home-made food production encouraging the growth of a virtuous microflora (i.e. addition of selected starter, backslopping) rather than uncontrolled spontaneous fermentation.

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Declaration of competing interest

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