



Microbiology and antimicrobial effects of kombucha, a short overview

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ARTICLE INFO

Keywords:

Fermentation
Microbiota
Nutrition
Antimicrobial effect

ABSTRACT

Kombucha is a beverage usually prepared with black or green tea containing sucrose, and a synbiotic culture of bacteria and yeasts (SCOBY). This paper aims at offering an overview on kombucha microbiota, as well as on its nutritional composition, and antimicrobial effects. The microbiota of kombucha includes acetic acid bacteria (*Acetobacter*, *Gluconobacter*, *Gluconacetobacter*, *Komagataeibacter*), lactic acid bacteria (*Lactobacillus*, *Lactiplantibacillus*, *Lactocaseibacillus*) and yeasts (*Brettanomyces*, *Candida*, *Saccharomyces*, *Zygosaccharomyces*), depending on raw materials, starter cultures, and fermentation temperature. The second topic of this review is the production path and kombucha composition, with a synopsis on a quali-quantitative point of view of the most important compounds. Finally, the review examines the antimicrobial potential, focusing on both Gram-positive and Gram-negative bacteria.

An open question is on the probiotic status of kombucha; this review offers a contribution to this debate, suggesting for this beverage the status of post-biotic.

1. Introduction

Kombucha, also defined as fermented tea, is a beverage usually prepared with black or green tea containing sucrose and a synbiotic culture of bacteria and yeasts (SCOBY), which varies between fermentations (Kruk et al., 2021). Generally, kombucha is composed of two phases, that is a floating biofilm layer and a sour liquid (Kruk et al., 2021).

SCOBY consists of acetic acid bacteria (*Komagataeibacter*, *Gluconobacter*, *Acetobacter* species) (AAB), lactic acid bacteria (*Lactobacillaceae*, *Lactococcus*) (LAB), bifidobacteria, and yeasts (*Schizosaccharomyces pombe*, *Saccharomycodes ludwigii*, *Kloeckera apiculata*, *Saccharomyces cerevisiae*, *Zygosaccharomyces bailii*, *Torulaspota delbrueckii*, *Brettanomyces bruxellensis*) (Kruk et al., 2021; Villarreal-Soto et al., 2019); however, there is a debate on the distinction between species essential for kombucha production and contaminant/not essential microorganisms (Harrison & Curtin, 2021). According to Coton et al. (2017), the viable count of bacteria and yeasts is at 6–7 log CFU/mL.

Some authors report a probiotic potential for kombucha, due to its high levels of LAB and bifidobacteria (Coton et al., 2017; Pei et al., 2020). However, the use of the term probiotic for kombucha has a big issue due to the high level of non-living microorganisms as a consequence

of a long fermentation processes and pasteurisation of commercial kombucha; therefore, it is more suitable to refer to kombucha as a postbiotic, which is defined by ISAPP (The International Scientific Association of Probiotics and Prebiotics) as “non-living microorganisms and/or their components that provide health benefits to the host” (Antolak et al., 2021). In addition, according to Hill et al. (2014) traditional fermented foods cannot be simply labeled as “probiotics”; the main requirement for a claim of “probiotic food” is the isolation and identification of strains with health-promoting effects.

There is an increasing number of papers focusing on kombucha, and an evaluation of the most important keywords and topics through VosViewer software reveals some areas of interest. The first one is on the chemistry, antioxidant activity, and effects on metabolism of kombucha (purple circles); a second area is on microbiology (green, blue, and yellow circles) with some topics covered (microbial consortia, end-products of fermentations, approaches for microorganisms' identification and characterization, use of starter cultures or natural fermentations), while the third area is on controlled studies to demonstrate the health effects of kombucha (Fig. 1).

Thus, this figure suggests that kombucha should be described and studied at different levels; therefore, the main aim of this review is to offer a synopsis on the existing knowledge on kombucha, with a focus on

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<https://doi.org/10.1016/j.fbio.2023.103270>

Received 29 July 2023; Received in revised form 10 October 2023; Accepted 11 October 2023

Available online 27 October 2023

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kombucha is not limited to a simple fermentation (Tran et al., 2020). Fermentation processes frequently observed in kombucha production can be classified as lactic acid fermentation, alcoholic fermentation by yeasts, and acetic acid fermentation (oxidation of carbohydrates and alcohols by acetic acid bacteria) (Kruk et al., 2021). Sucrose at a concentration of 5%–20% is the primary carbon source (Martínez Leal et al., 2018), and is hydrolysed to glucose and fructose via invertase enzyme. This step explains the symbiosis observed in kombucha due to the inability of AAB to metabolise monosaccharides to produce organic acids (Neffe-Skocińska et al., 2017). As the system is in contact with oxygen, AAB produce acetic and gluconic acids (Chakravorty et al., 2016; Martínez Leal et al., 2018). Then, they convert gluconic acid into glucuronic acid, which has various health benefits (Lee, Jo, et al., 2021; Villarreal-Soto et al., 2019).

Finally, LAB either produce lactic acid by utilising glucose via the Embden-Meyerhof-Parnas pathway or lactic acid, ethanol, and carbon dioxide via the pentose phosphate pathway (Antolak et al., 2021).

3. Nutritional and chemical composition

Kombucha contains various enzymes (phytase, α -glycosidase, tannase), organic acids (acetic, gluconic, formic, glucuronic, lactic, oxalic, tartaric, malic, and citric acids), vitamins B₁, B₂, B₆, B₁₂ and C, ethanol, polyphenols (gallic acid derivatives), copper, iron, manganese, zinc, nickel, F⁻, Cl⁻, Br⁻, I⁻, NO₃⁻, HPO₄⁻, SO₄⁻ anions (Kaewkod et al., 2019; Mousavi et al., 2020; Villarreal-Soto et al., 2019). The most important polyphenols are theaflavin, thearubigin, and caffeine; a key-compound is also d-saccharic acid-1,4-lactone (DSL), whose concentration depends on the raw material (Chakravorty et al., 2016). Enzymes such as phytase, α -glycosidase, and tannase, which are active during the fermentation of kombucha, are crucial for the degradation of complex polyphenols into small phenolic compounds (Kaewkod et al., 2019), thus increasing the bioavailability of tea polyphenols (Tamer et al., 2021).

Generally, the bioavailability of polyphenols increases as a result of the conjugation of glucuronic acid with tea polyphenols (Martínez Leal et al., 2018).

Various health protective effects of glucuronic acid (GlcUA) and DSL have been reported (Lee, Jo, et al., 2021). DSL has hypocholesterolaemic, hepatoprotective, and antihyperglycaemic effects (Emiljanowicz & Malinowska-Pańczyk, 2020; Özdemir & Çon, 2017), while GlcUA is a precursor of vitamin C, and has several functions (toxin dextoxification, increase of the bioavailability of phenolic compounds by taking part in glucuronidation, and reduction of oxidative damage). In addition, vitamin C, polyphenols, and lactic acid in kombucha, together with GlcUA, play a role in reducing gastric cancer proliferation (Kitwetcharoen et al., 2023). An overview of kombucha composition is in Table 1.

4. Microbial community and dominant species of kombucha

There is not a single formula that describes the microbiota of kombucha, because it depends mainly on the starter cultures used in fermentation, but also on the raw materials (plants and other ingredients), the amount of sucrose, the fermentation temperature, and the duration of the process (Diez-Ozaeta & Astiazaran, 2022). It is worth mentioning that kombucha fermentation takes place mainly in the presence of AAB and yeast, although variations in bacteria or yeasts species are observed (Chakravorty et al., 2016), while LAB presence is not a *sine qua non conditio*, although they constitute an important part of the microbiota of kombucha (Coton et al., 2017; Nguyen, Dong, et al., 2015).

As reported in the introduction, the microbiota of SCOBY is a driver for the composition of the microbiota of kombucha. In a study examining the microbial content of five different SCOBYs, *Gluconacetobacter* was the predominant genus; in addition, low levels of *Acetobacter* were

Table 1
Chemical composition of kombucha.

Compound		Amount										
Vitamins	Vitamin C	1.51 mg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a										
		25–30 mg/L, and 8–10 mg/L (Malbaša et al., 2011) ^b										
		~0.25–1.00 mg/100 mL (Lončar et al., 2006) ^c										
		0.40–1.20 mg/L (Vitas et al., 2018) ^d										
		0.02 mg/100 g (Phung et al., 2023) ^e										
		0.14–6.95 mg/mL (Klawpiyapamornkun et al., 2023) ^f										
		0.60–0.70 g/L (Kaewkod et al., 2019) ^{www}										
		1.55 g/L (Ivanišová et al., 2019) ^{9a}										
		0.74 mg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a										
		0.05 mg/100 g (Phung et al., 2023) ^e										
		8–10 mg/100 mL (Malbaša et al., 2011) ^b										
		ND (Phung et al., 2023) ^e										
Vitamins	Thiamine	0.07 mg/100 g (Phung et al., 2023) ^e										
		0.52 mg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a										
		0.01 mg/100 g (Phung et al., 2023) ^e										
		0.01 mg/100 g (Phung et al., 2023) ^e										
		0.84 mg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a										
		ND (Phung et al., 2023) ^e										
		Vitamins	Riboflavin	31.24 mg/kg (Phung et al., 2023) ^e								
				0.07 g/100 g (Jayabalan et al., 2010) ^g								
				0.462 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a								
				1.57 mg/L (Ivanišová et al., 2019) ^{9a}								
				63.78 mg/kg (Phung et al., 2023) ^e								
				0.02 g/100 g (Jayabalan et al., 2010) ^g								
Vitamins	Niacin			77.80 mg/kg (Phung et al., 2023) ^e								
				0.40 g/100 g (Jayabalan et al., 2010) ^g								
				991.95 mg/kg (Phung et al., 2023) ^e								
				0.17 g/100 g (Jayabalan et al., 2010) ^g								
				Vitamins	Pyridoxine	16.96 mg/kg (Phung et al., 2023) ^e						
						0.30 g/100 g (Jayabalan et al., 2010) ^g						
		72.30 mg/kg (Phung et al., 2023) ^e										
		0.03 g/100 g (Jayabalan et al., 2010) ^g										
		Vitamins	Folic acid			7.60 mg/kg (Phung et al., 2023) ^e						
						0.05 g/100 g (Jayabalan et al., 2010) ^g						
						0.353 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a						
						0.31 mg/L (Ivanišová et al., 2019) ^{9a}						
Vitamins	Cyanocobalamin					1.4 g/kg (Phung et al., 2023) ^e						
						0.346 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a						
						0.42 mg/L (Ivanišová et al., 2019) ^{9a}						
						20.85 mg/kg (Phung et al., 2023) ^e						
				Vitamins	Cyanocobalamin	0.237 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a						
						0.14 mg/L (Ivanišová et al., 2019) ^{9a}						
						71.75 mg/kg (Phung et al., 2023) ^e						
						0.09 g/100 g (Jayabalan et al., 2010) ^g						
		Minerals	Manganese			0.154 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a						
						0.53 mg/L (Ivanišová et al., 2019) ^{9a}						
						0.04 g/100 g (Jayabalan et al., 2010) ^g						
						0.12 g/100 g (Jayabalan et al., 2010) ^g						
Minerals	Phosphorus					0.005 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a						
						0.12 mg/L (Ivanišová et al., 2019) ^{9a}						
						0.004 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a						
						0.23 mg/L (Ivanišová et al., 2019) ^{9a}						
				Minerals	Magnesium	0.001 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a						
						ND (Ivanišová et al., 2019) ^{9a}						
						Minerals	Potassium	0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a				
								ND (Ivanišová et al., 2019) ^{9a}				
		Minerals	Sodium					0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a				
								0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a				
								Minerals	Iron	0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a		
										0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a		
Minerals	Nitrogen									0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a		
										0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a		
										Minerals	Nickel	0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
				Minerals	Copper							0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
						Minerals	Zinc					0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
		Minerals	Chlorine									0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
								Minerals	Sulphur			0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
Minerals	Lead											0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
										Minerals	Cobalt	0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
				Minerals	Chromium							0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
						Minerals	Cadmium					0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a
												0.00 µg/mL (Bauer-Petrovska & Petrushevska-Tozi, 2000) ^a

(continued on next page)

Table 1 (continued)

Compound	Amount
Polyphenols	Total
	206.0–320.1 mg/L (Jakubczyk et al., 2020) ^h
	Isorhamnetin
	156.38 µg/mL (Bhattacharya et al., 2016) ^s
	Catechin
	0.05–2.00 mg/L (Gaggia et al., 2018) ⁱ
	0.3–1.5 µg/mL (Yang et al., 2022) ^y
	68.17 µg/mL (Bhattacharya et al., 2016) ^s
	(–)-epicatechin
	1.3–11.6 µg/mL (Yang et al., 2022) ^y
	0.05–50.0 mg/L (Gaggia et al., 2018) ⁱ
	~10.0–250.0 mg/L (Zhou et al., 2022) ^w
	(–)-epicatechin gallate
	4.7–32.1 µg/mL (Yang et al., 2022) ^y
	0.05–1.0 mg/L (Gaggia et al., 2018) ⁱ
	~2.5–225.0 mg/L (Zhou et al., 2022) ^w
	(–)-epigallocatechin
	0.1–80.0 mg/L (Gaggia et al., 2018) ⁱ
	(–)-epigallocatechin gallate
	7.0–51.1 µg/mL (Yang et al., 2022) ^y
	12.5–50.0 mg/L (Gaggia et al., 2018) ⁱ
	20.24 µg/mL (La Torre et al., 2021) ^l
	~200.0–600.0 mg/L (Zhou et al., 2022) ^w
	(+)-gallocatechin
	0.1–5.0 mg/L (Gaggia et al., 2018) ⁱ
	~40.0–120.0 mg/L (Zhou et al., 2022) ^w
	Gallocatechin gallate
	~10.0–20.0 mg/L (Zhou et al., 2022) ^w
	Vitexin
	1.91 µg/mL (Ivanišová et al., 2019) ^u
	Rutin
	13.35 µg/mL (Ivanišová et al., 2019) ^u
	Syringic acid
	4.51 µg/mL (Ivanišová et al., 2019) ^u
	Galic acid
	30.23 µg/mL (Ivanišová et al., 2019) ^u
	~35.0–80.0 mg/L (Zhou et al., 2022) ^w
	Ferulic acid
	0.33 µg/mL (Ivanišová et al., 2019) ^u
	2.97 µg/mL (La Torre et al., 2021) ^l
	Ellagic acid
	1.93 µg/mL (Ivanišová et al., 2019) ^u
	~4.0–11.0 mg/L (Zhou et al., 2022) ^w
	p-Coumaric acid
	0.79 µg/mL (Ivanišová et al., 2019) ^u
	Protocatechuic acid
	2.11 µg/mL (Ivanišová et al., 2019) ^u
	Chlorogenic acid
	14.86 µg/mL (Ivanišová et al., 2019) ^u
	29.60 µg/mL (La Torre et al., 2021) ^l
	Quercetin
	ND (La Torre et al., 2021) ^l
	Quercitrin
	~3.0–9.0 mg/L (Zhou et al., 2022) ^w
	Myricetin
	~1.25–2.0 mg/L (Zhou et al., 2022) ^w
	Astragalgin
	~5.0–20.0 mg/L (Zhou et al., 2022) ^w
Alcohol	
	0.15%–0.40% (Alderson et al., 2021) ^j
	2.0%–3.0% (Jakubczyk et al., 2020) ^h
	0.4% (Ivanišová et al., 2019) ^u
	Ethanol
	0.09%–0.99% (v/v) (Phung et al., 2023) ^e
	1.14–5.83 mg/mL (Gaggia et al., 2018) ⁱ
	0.59%–0.84% (v/v) (Akbarirad et al., 2017) ^k
	1.00–4.00 g/L (Tanticharakunsiri et al., 2021) ^x
	0.93–4.4 g/L (Velicanski et al., 2013) ^{xx}
	0.00%–1.30% (Yang et al., 2022) ^y
	0.14 g/L (Chakravorty et al., 2016) ^z
	1.04%–1.01% (Coton et al., 2017) ^o
	3.28 mmol/L (Tan et al., 2020) ^p
Sugars	Glucose
	22.93 g/100 g (Phung et al., 2023) ^e
	15.12–18.10 mg/mL (Gaggia et al., 2018) ⁱ
	~1.00–2.00 g/L (Lončar et al., 2006) ^c
	4.60 mmol/L (Tan et al., 2020) ^p
	9.35 g/L (Ivanišová et al., 2019) ^u
	18.87 g/100 g (Phung et al., 2023) ^e
	5.50–8.83 mg/mL (Gaggia et al., 2018) ⁱ
	~0.75–3.20 g/L (Lončar et al., 2006) ^c
	21.01 mmol/L (Tan et al., 2020) ^p
	1.41 g/L (Ivanišová et al., 2019) ^u
	10.80 g/100 g (Phung et al., 2023) ^e
	Fructose
	18.87 g/100 g (Phung et al., 2023) ^e
	5.50–8.83 mg/mL (Gaggia et al., 2018) ⁱ
	~0.75–3.20 g/L (Lončar et al., 2006) ^c
	21.01 mmol/L (Tan et al., 2020) ^p
	1.41 g/L (Ivanišová et al., 2019) ^u
	10.80 g/100 g (Phung et al., 2023) ^e
	Sucrose
	10.80 g/100 g (Phung et al., 2023) ^e

Table 1 (continued)

Compound	Amount
	26.13–33.65 mg/mL (Gaggia et al., 2018) ⁱ
	7.5–9.5 g/100 mL (Jakubczyk et al., 2020) ^h
	2.3–7.2 g/100 mL (Akbarirad et al., 2017) ^k
	~22.5–32.5 g/L (Lončar et al., 2006) ^c
	11.51 mmol/L (Tan et al., 2020) ^p
	17.81 g/L (Ivanišová et al., 2019) ^u
Organic acids	Acetic acid
	20.90%–46.06% (Phung et al., 2023) ^e
	4.34–6.70 mg/mL (Abou-Taleb et al., 2017) ^l
	4.89–9.18 mg/mL (Gaggia et al., 2018) ⁱ
	9071.02–9147.40 mg/L (Jakubczyk et al., 2020) ^h
	3.4–3.8 g/100 mL (Akbarirad et al., 2017) ^k
	16.71–78.28 mg/mL (Klawpiyapamornkun et al., 2023) ^f
	~6.0–14.0 g/L (Wang et al., 2022) ^m
	0.32–2.25 g/L (Utoiu et al., 2018) ⁿ
	12.53 g/L (Chakravorty et al., 2016) ^z
	8.17–15.72 mmol/L (Coton et al., 2017) ^o
	0.33 mmol/L (Tan et al., 2020) ^p
	12.53 mg/mL (Bhattacharya et al., 2013) ^f
	5.77 g/L (Tu et al., 2019) ^f
	10.42–11.15 g/L (Kaewkod et al., 2019) ^{ww}
	1.55 g/L (Ivanišová et al., 2019) ^u
	1131.8–2755.8 mg/L (Shahbazi et al., 2018) ^{zz}
	Citric acid
	590.00 mg/100 g (Phung et al., 2023) ^e
	~0.5–1.0 g/L (Wang et al., 2022) ^m
	1.07 g/L (Tu et al., 2019) ^f
	0.05 g/L (Ivanišová et al., 2019) ^u
	39.22–471.58 mg/L (Shahbazi et al., 2018) ^{zz}
	Formic acid
	ND (Phung et al., 2023) ^e
	0.78 g/L (Tu et al., 2019) ^f
	Gluconic acid
	6.93–15.35 mg/mL (Klawpiyapamornkun et al., 2023) ^f
	0.94–2.55 g/L (Utoiu et al., 2018) ⁿ
	6.38 g/L (Chakravorty et al., 2016) ^z
	0.15–0.20 mmol/L (Coton et al., 2017) ^o
	6.59 mmol/L (Tan et al., 2020) ^p
	6.38 mg/mL (Bhattacharya et al., 2013) ^f
	41.42–70.11 g/L (Kaewkod et al., 2019) ^{ww}
	Glucuronic acid
	1.96–3.23 mg/mL (Gaggia et al., 2018) ⁱ
	ND (Klawpiyapamornkun et al., 2023) ^f
	0.05 mmol/L (Coton et al., 2017) ^o
	2.30 g/L (Tu et al., 2019) ^f
	0.07–1.58 g/L (Kaewkod et al., 2019) ^{ww}
	118.92–1158.2 mg/L (Shahbazi et al., 2018) ^{zz}
	0.44–1.26 mg/mL (Klawpiyapamornkun et al., 2023) ^f
	1.32 g/L (Chakravorty et al., 2016) ^z
	1.34 mg/mL (Bhattacharya et al., 2013) ^f
	3.44–5.23 g/L (Kaewkod et al., 2019) ^{ww}
	Lactic acid
	~0.2–0.3 g/L (Wang et al., 2022) ^m
	0.37–0.72 g/L (Utoiu et al., 2018) ⁿ
	15.37–10.46 mmol/L (Coton et al., 2017) ^o

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Table 1 (continued)

Compound	Amount
	90.81–269.83 mg/L (Shahbazi et al., 2018) ^{zz}
Oxalic acid	~0.05–0.2 g/L (Wang et al., 2022) ^{mm} 8.4–24.8 mg/L (Shahbazi et al., 2018) ^{zz}
Tartaric acid	~0.1–0.2 g/L (Wang et al., 2022) ^{mm} 0.23 g/L (Ivanišová et al., 2019) ^{qq} 16.8–73.4 mg/L (Shahbazi et al., 2018) ^{zz}
Pyruvic acid	~0.05–0.1 g/L (Wang et al., 2022) ^{mm}
Malic acid	~1.8–3.0 g/L (Wang et al., 2022) ^{mm} 0.13 mmol/L (Tan et al., 2020) ^p 89.0–312.0 mg/L (Shahbazi et al., 2018) ^{zz}
α-ketoglutaric acid	~0.1–0.5 g/L (Wang et al., 2022) ^{mm}
Succinic acid	~0.2–0.3 g/L (Wang et al., 2022) ^{mm} 3.05 g/L (Kaewkod et al., 2019) ^{www}
Citric acid	~0.5–0.1 g/L (Wang et al., 2022) ^{mm} ND – 0.04 g/L (Utoiu et al., 2018) ⁿ
Propionic acid	0.16–0.42 g/L (Utoiu et al., 2018) ⁿ
Butyric acid	0.28–1.06 g/L (Utoiu et al., 2018) ⁿ
Caffeine	100.72 µg/mL (Ivanišová et al., 2019) ⁱⁱ 39.00 µg/mL (Miranda et al., 2016) ^v 15.1–112.6 µg/mL (Yang et al., 2022) ^y 0.713 g/L (Chakravorty et al., 2016) ^z 356.25 µg/mL (La Torre et al., 2021) ^q ~80.0–175.0 mg/L (Zhou et al., 2022) ^w
Amino acids	Isoleucine 35.2 mg/g (Jayabalan et al., 2010) ^g Leucine 35.9 mg/g (Jayabalan et al., 2010) ^g Lysine 48.0 mg/g (Jayabalan et al., 2010) ^g Methionine 11.3 mg/g (Jayabalan et al., 2010) ^g Phenylalanine 22.3 mg/g (Jayabalan et al., 2010) ^g Threonine 13.2 mg/g (Jayabalan et al., 2010) ^g Valine 22.3 mg/g (Jayabalan et al., 2010) ^g Tryptophan 12.3 mg/g (Jayabalan et al., 2010) ^g Alanine 41.9 mg/g (Jayabalan et al., 2010) ^g Arginine 30.8 mg/g (Jayabalan et al., 2010) ^g Aspartic acid 42.0 mg/g (Jayabalan et al., 2010) ^g Cysteine 15.2 mg/g (Jayabalan et al., 2010) ^g Glutamic acid 42.3 mg/g (Jayabalan et al., 2010) ^g Glycine 17.2 mg/g (Jayabalan et al., 2010) ^g Histidine 10.6 mg/g (Jayabalan et al., 2010) ^g Proline 35.2 mg/g (Jayabalan et al., 2010) ^g Serine 22.2 mg/g (Jayabalan et al., 2010) ^g Tyrosine 18.6 mg/g (Jayabalan et al., 2010) ^g
Enzymes	Mn-SOD + (Tanticharakunsiri et al., 2021) ^x Catalase + (Tanticharakunsiri et al., 2021) ^x GRe + (Tanticharakunsiri et al., 2021) ^x

Table footnotes.

- ^a Black tea kombucha, 6–15 days of fermentation.
^b Black tea kombuchas, 10th day of fermentation.
^c Black tea kombuchas, 10th day of fermentation.
^d Yarrow kombuchas, 7th day of fermentation.
^e Black tea kombuchas with and without different amounts of pineapple peel and seed, 14th day of fermentation.
^f Green tea kombuchas with and without Indian gooseberry supplement, 21st day of fermentation.
^g Dried tea fungus, 14th day of fermentation of black tea.
^h White, green, black and red tea kombuchas, 14th day of fermentation.
ⁱ Green tea, black tea and rooibos tea kombuchas, 14th day of fermentation.
^j Black tea, kawakawa (*Piper excelsum*) leaves, hops and black pepper kombuchas, 7th day of fermentation.
^k Pomegranate, red grape, sour cherry and apple juice kombuchas, 14th day of fermentation.
^l Black tea, rice and barley kombuchas, 8th and 10th day of fermentation.
^m Black and green tea kombuchas, 15th day of fermentation.
ⁿ Green tea kombuchas with and without pollen, 13th day of fermentation.
^o Green and black tea kombuchas, 8th day of fermentation.
^p Black tea with soursop juice kombucha, 14th day of fermentation.
^r Black tea kombucha, 14th day of fermentation.
^s Black tea kombucha, 14th day of fermentation.

- ^t Black tea with soy whey kombucha, 7th day of fermentation.
^u Black tea kombucha, 7th day of fermentation.
^v Black tea kombucha, 14th day of fermentation.
^y Commercial kombuchas of black tea, green tea, or both, and/various flavoring ingredients, unknown fermentation day.
^z Black tea kombucha, 14th day of fermentation.
^q Black tea kombucha, 30th day of fermentation.
^w Green and black tea kombuchas, 15th day of fermentation.
^x Mint and oolong tea kombuchas, 14th day of fermentation.
^{xx} Kombucha from medicinal herbs belonging to Lamiaceae family: lemon balm, thyme, peppermint and sage, 5–12 days of fermentation.
^{www} Green tea, oolong tea, and black tea kombuchas, 15th day of fermentation.
^{qq} Black tea kombucha, 7th day of fermentation.
^{zz} Green tea with cinnamon, cardamom, and Shirazi thyme kombuchas, 16th day of fermentation.

found, while *Lactobacillus* could be recovered at high frequencies. *Komagataeibacter*, *Acetobacter*, *Gluconobacter*, and *Gluconacetobacter* were the most important AAB, with a major role of *K. intermedius*, *K. rhaeticus*, *K. saccharivorans*, *K. hanseni*, *A. xylinum*, *A. aceti*, *A. pasteurians*, *A. tropicalis*, and *G. oxydans* at species level (Table 2) (Arkan et al., 2020; De Filippis et al., 2018; Gaggia et al., 2018; Reva et al., 2015).

LAB are very important for the production of DSL (Nguyen, Nguyen, et al., 2015), mainly lactobacilli and lactococci, as shown in Table 2 (De Filippis et al., 2018; Lee, Jo, et al., 2021).

Yeasts biota includes *Brettanomyces*, *Hanseniaspora*, *Saccharomyces*, *Schizosaccharomyces*, *Dekkera*, *Zygosaccharomyces*, *Pichia*, *Candida*, and *Lachancea* (Chakravorty et al., 2016; Landis et al., 2022; Marsh et al., 2014; Tran et al., 2021), with a high recovery of *B. bruxellensis*, *H. valbyensis*, *S. cerevisiae*, *Schizo. pombe*, *D. anomala*, and *Z. bailii* (Table 2).

The strong differences in kombucha microbiota probably depend on the different approaches or protocols used, as well as on the different kinds of kombucha and sampling time. However, some useful information could be gained from Marsh et al. (2014), who used a metagenomic approach to analyse the microbiota of kombucha. They identified five main bacterial phyla, including Actinobacteria, Bacteroidetes, *Deinococcus-Thermus*, Firmicutes, and Proteobacteria. Focusing on the data after 10 days, the genus mainly represented in all samples was *Gluconacetobacter*, with lower recovery frequencies of lactobacilli (Fig. 3). The same trend was found for biofilm, with just one sample difference. Yeast biota was mainly represented by *Zygosaccharomyces* spp. (79%–99%).

The importance of AAB and their dominance was highlighted also by Kaashyap et al. (2021), who found that the genus mostly represented was *Acetobacter* spp., followed by *Komagataeibacter*, and *Gluconobacter*.

From a quantitative point of view, the levels of the different groups are highly variable, depending on the raw material, as well as on the methodologies used by the researchers to perform experiments. Nevertheless it was possible to find some details from various bibliographic references and build a violin plot (Fig. 4). This graph is a powerful tool for the visualization of data from both small-sized and high-sized samples, and enables the reader to understand whether data distribution follows a normal trend, or if it is unimodal, or multimodal. The plot highlights the high variability of AAB levels (5.5–8.5 log CFU/mL in green tea and 4.5–8.5 log CFU/mL in black tea kombucha); a certain degree of variability was also found for yeasts (6.0–8.0 log CFU/mL), and for LAB in green tea kombucha (5.8–8.0 log CFU/mL), while the variability was lower for LAB in black tea kombucha (5.5–6.5 log CFU/mL).

5. Probiotic microorganisms from kombucha

Kombucha has several health-promoting effects, including antioxidant, antitumor, anti-inflammatory, antihypertensive, antidiabetic, hypocholesteremic, and hepatoprotective properties, as well as the ability to modulate gut microbiota (Diez-Ozaeta & Astiazaran, 2022; Moreira et al., 2022; Permatasari et al., 2022), but it is controversial

Table 2
Microbiota of kombucha.

GENUS	SPECIES	TYPE OF KOMBUCHA	REFERENCES	
ACETIC ACID BACTERIA				
<i>Acetobacter</i>	spp.	Green and black tea, biofilm	(De Filippis et al., 2018; Fabricio et al., 2022; Góes-Neto et al., 2021; Marsh et al., 2014; Watawana et al., 2016)	
	<i>indonesiensis</i>	Black and green tea	Tran et al. (2022)	
	<i>xylinum</i>	Black tea	(Al-Mohammadi et al., 2021; Sievers et al., 1995)	
	<i>aceti</i>	Black tea	(Al-Mohammadi et al., 2021; Sievers et al., 1995)	
	<i>pasteurianus</i>	Green and black tea	(Al-Mohammadi et al., 2021; Landis et al., 2022; Sievers et al., 1995)	
	<i>lovaniensis</i>	Green tea	Coton et al. (2017)	
	<i>okinawensis</i>	Black and green tea	Coton et al. (2017)	
	<i>peroxydans</i>	Green tea	Coton et al. (2017)	
	<i>syzygii</i>	Green tea	Coton et al. (2017)	
	<i>tropicalis</i>	Green and black tea	Coton et al. (2017)	
		Green tea	Landis et al. (2022)	
	<i>senegalensis</i>	Green tea	Landis et al. (2022)	
	<i>pomorum</i>	Green tea	Landis et al. (2022)	
	<i>musti</i>	Green tea	Landis et al. (2022)	
	<i>nitrogenifigens</i>	No data available (reported as only “kombucha”)	Dutta and Gachhui (2006)	
	<i>Gluconobacter</i>	<i>papayae</i>	Black tea	Tran et al. (2021)
		spp.	Black tea	(Chakravorty et al., 2016; Fabricio et al., 2022; Reva et al., 2015)
		<i>entanii</i>	Rooibos, green tea	Gaggia et al. (2018)
		<i>oxydans</i>	Black tea, green tea, lemon verbena, mallow, wild rose, peppermint	(Grassi et al., 2022; Lee, Jo, et al., 2021; Podolich et al., 2017; Reva et al., 2015; Villarreal-Soto et al., 2020)
<i>Gluconacetobacter</i>	spp.	Green and black tea, biofilm,	(Arkan et al., 2020; De Filippis et al., 2018; Fabricio et al., 2022; Góes-Neto et al., 2021; Landis et al., 2022; Marsh et al., 2014; Villarreal-Soto et al., 2020; Watawana et al., 2016)	
	<i>saccharivorans</i>	Green and black tea	De Filippis et al. (2018)	

Table 2 (continued)

GENUS	SPECIES	TYPE OF KOMBUCHA	REFERENCES
<i>Komagataeibacter</i>	<i>xylinus</i>	Green and black tea	De Filippis et al. (2018)
	<i>europaeus</i>	Green and black tea	Coton et al. (2017)
	<i>hansenii</i>	Black tea	Coton et al. (2017)
	<i>intermedius</i>	Green and black tea	Coton et al. (2017)
	<i>liquefaciens</i>	Black tea	Coton et al. (2017)
	<i>xylinus</i>	Green tea	Coton et al. (2017)
	<i>takamatsuzukensis</i>	Black tea	Tran et al. (2021)
	<i>diazotrophicus</i>	Black tea	Reva et al. (2015)
	<i>entanii</i>	Black tea	Reva et al. (2015)
	<i>cerinus</i>	Black tea	Coton et al. (2017)
	<i>oxydans</i>	Green and black tea	(Coton et al., 2017; Landis et al., 2022)
	spp.	Rooibos, green tea, black tea	(Arkan et al., 2020; Chakravorty et al., 2016; Fabricio et al., 2022; Gaggia et al., 2018; Góes-Neto et al., 2021; Podolich et al., 2017)
	<i>intermedius</i>	Rooibos, green tea, black tea	(Gaggia et al., 2018; Landis et al., 2022; Reva et al., 2015; Villarreal-Soto et al., 2020)
	<i>rhaeticus</i>	Rooibos, green and black tea	(Arkan et al., 2020; Gaggia et al., 2018; Góes-Neto et al., 2021; Landis et al., 2022; Lee, Barh, et al., 2021; Semjonovs et al., 2017; Villarreal-Soto et al., 2020)
	<i>saccharivorans</i>	Rooibos, green tea, black tea, lemon, verbena, mallow, wild rose, peppermint	(Gaggia et al., 2018; Góes-Neto et al., 2021; Grassi et al., 2022; Landis et al., 2022; Mukadam et al., 2016)
<i>xylinus</i>	Green and black tea	(Landis et al., 2022; Reva et al., 2015; Villarreal-Soto et al., 2020)	
<i>hansenii</i>	Green tea and black tea	(Góes-Neto et al., 2021; Landis et al., 2022; Lee et al., 2021a, 2021b; Semjonovs et al., 2017)	
<i>swingsii</i>	Green tea	Landis et al. (2022)	
<i>europaeus</i>	Green and black tea	(Landis et al., 2022; Villarreal-Soto et al., 2020)	
<i>medellinensis</i>	Green tea	Landis et al. (2022)	
<i>cocois</i>	Green tea	Landis et al. (2022)	
<i>diospyri</i>	Green tea	Landis et al. (2022)	
<i>nataicola</i>	Green and black tea	(Landis et al., 2022; Reva et al., 2015)	

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Table 2 (continued)

GENUS	SPECIES	TYPE OF KOMBUCHA	REFERENCES
Novacetimonas	<i>oboediens</i>	Black tea	Lee, Barh, et al. (2021)
	<i>hansenii</i>	Green tea, lemon verbena, mallow, wild rose, peppermint	Grassi et al. (2022)
<i>Tanticharoemia</i>	<i>sakaeratensis</i>	Green tea	Coton et al. (2017)
LACTIC ACID BACTERIA			
<i>Enterococcus</i>	<i>faecium</i>	Green tea	Landis et al. (2022)
<i>Lactobacillus</i>	spp.	Black tea, biofilm	(Chakravorty et al., 2016; Lee, Jo, et al., 2021; Marsh et al., 2014; Watawana et al., 2016)
	<i>delbrueckii</i>	Black tea	Lee, Jo, et al. (2021)
	<i>acidophilus</i>	Black tea	Al-Mohammadi et al. (2021)
<i>Lacticaseibacillus</i>	<i>casei</i>	Black tea	Lee, Jo, et al. (2021)
<i>Lactiplantibacillus</i>	<i>plantarum</i>	Green tea	Landis et al. (2022)
<i>Ligilactobacillus</i>		Black tea	Fabricio et al. (2022)
<i>Limosilactobacillus</i>	<i>fermentum</i>	Black tea	Al-Mohammadi et al. (2021)
<i>Lactococcus</i>	spp.	Green, black tea, biofilm	Marsh et al., 2014; De Filippis et al., 2018; Watawana et al., 2016
<i>Liquorilactobacillus</i>	spp.	Black tea	Fabricio et al. (2022)
	<i>ghanensis</i>	Green tea	Landis et al. (2022)
	<i>nagelii</i>	Green and black tea	(Coton et al., 2017; Landis et al., 2022)
<i>Leuconostoc</i>	<i>satsumensis</i>	Green tea	Coton et al. (2017)
	spp.	Biofilm	Watawana et al. (2016)
<i>Oenococcus</i>	<i>oeni</i>	Green and black tea	(Coton et al., 2017; Lee, Jo, et al., 2021)
<i>Sporolactobacillus</i>	<i>shoreae</i>	Black tea	(Lee, Jo, et al., 2021)
<i>Streptococcus</i>	spp.	Green and black tea	De Filippis et al. (2018)
<i>Weissella</i>	spp.	Black tea	Chakravorty et al. (2016)
OTHER BACTERIA			
<i>Acidomonas</i>	<i>methanolica</i>	Green tea	Landis et al. (2022)
<i>Acidiphilium</i>	spp.	Black tea	Góes-Neto et al. (2021)
<i>Bifidobacterium</i>	spp.	Black tea and biofilm	Chakravorty et al., 2016; Watawana et al., 2016
	<i>bifidum</i>	Black tea	(Lee, Jo, et al., 2021)
	<i>longum</i>	Black tea	(Lee, Jo, et al., 2021)
<i>Burkholderia</i>	spp.	Black tea	(Góes-Neto et al., 2021; Reva et al., 2015)
<i>Collinsella</i>	spp.	Black tea	Chakravorty et al. (2016)
<i>Corynebacterium</i>	spp.	Green and black tea	De Filippis et al. (2018)
<i>Enterobacter</i>	spp.	Black tea	Chakravorty et al. (2016)
<i>Herbaspirillum</i>	spp.	Black tea	Reva et al. (2015)
	<i>putei</i>	Black tea	Reva et al. (2015)
<i>Halomonas</i>	spp.	Black tea	Reva et al. (2015)

Table 2 (continued)

GENUS	SPECIES	TYPE OF KOMBUCHA	REFERENCES
<i>Propionibacterium</i>	<i>phocaea</i>	Black tea	Reva et al. (2015)
	spp.	Green and black tea	De Filippis et al. (2018)
<i>Pseudomonas</i>	spp.	Black tea	(Góes-Neto et al., 2021; Lee, Barh, et al., 2021)
<i>Ralstonia</i>	<i>pickettii</i>	Black tea	(Lee, Jo, et al., 2021)
<i>Shewanella</i>	<i>algae</i>	Black tea	Reva et al. (2015)
	<i>haliotis</i>	Black tea	Reva et al. (2015)
<i>Zymomonas</i>	spp.	Black tea	Fabricio et al. (2022)
YEASTS			
<i>Brettanomyces/Dekkera</i>	spp.	Black tea, biofilm	Góes-Neto et al., 2021; Marsh et al., 2014; Watawana et al., 2016; Fabricio et al., 2022
	<i>anomala</i>	Green and black tea, lemon verbena, mallow, wild rose, peppermint	Grassi et al., 2022; Coton et al., 2017; Podolich et al., 2017; Reva et al., 2015
	<i>bruxellensis</i>	Black tea, rooibos	(Coton et al., 2017; Gaggia et al., 2018; Landis et al., 2022; Tran et al., 2022)
	<i>naardenensis</i>	Green and black tea	Landis et al. (2022)
<i>Candida</i>	spp.	Black tea	(Góes-Neto et al., 2021; Reva et al., 2015)
	<i>boidinii</i>	Green and black tea	Coton et al. (2017)
	<i>parapsilosis</i>	Black tea	Chakravorty et al. (2016)
	<i>stellata</i>	Black tea	Teoh et al. (2004)
	<i>stellimalicola</i>	Black tea	Chakravorty et al. (2016)
	<i>tropicalis</i>	Black tea	Chakravorty et al. (2016)
<i>Debaryomyces</i>	<i>hansenii</i>	Black tea	Chakravorty et al. (2016)
<i>Eremothecium</i>	<i>cymbalariae</i>	Black tea	Chakravorty et al. (2016)
	<i>ashbyii</i>	Black tea	Chakravorty et al. (2016)
<i>Hanseniaspora</i>	spp.	Black tea	Fabricio et al. (2022)
	<i>meyeri</i>	Black tea	Chakravorty et al. (2016)
	<i>uvarum</i>	Black tea	Chakravorty et al. (2016)
	<i>valbyensis</i>	Green and black tea	Coton et al., 2017; Tran et al., 2021, 2022
	<i>vineae</i>	Black tea	Chakravorty et al. (2016)
<i>Kazachstania</i>	spp.	Black tea	Marsh et al. (2014)
	<i>exigua</i>	Black tea	Chakravorty et al. (2016)
	<i>telluris</i>	Black tea	Chakravorty et al. (2016)
<i>Kluyveromyces</i>	<i>marxianus</i>	Black tea	Chakravorty et al. (2016)
<i>Lachancea</i>	spp.	Black tea	Góes-Neto et al. (2021)
	<i>fermentati</i>	Black tea or other unspecified matrices	Chakravorty et al. (2016)

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Table 2 (continued)

GENUS	SPECIES	TYPE OF KOMBUCHA	REFERENCES
	<i>kluyveri</i>	Black tea	Chakravorty et al. (2016)
	<i>thermotolerans</i>	Black tea	Chakravorty et al. (2016)
<i>Leucosporidiella</i>	spp.	Black tea kombucha biofilm	Marsh et al. (2014)
<i>Merimbla</i>	<i>ingelheimense</i>	Black tea	Chakravorty et al. (2016)
<i>Meyerozyma</i>	<i>caribbica</i>	Black tea	Chakravorty et al. (2016)
	<i>guilliermondii</i>	Black tea	Chakravorty et al. (2016)
<i>Pichia</i>	spp.	Black tea and biofilm	Watawana et al. (2016)
	<i>occidentalis</i>	Black tea	Reva et al. (2015)
	<i>cecembensis</i>	Black tea	Reva et al. (2015)
	<i>fermentans</i>	Black tea	Reva et al. (2015)
	<i>membranifaciens</i>	Green and Black tea	(Coton et al., 2017; Landis et al., 2022)
	<i>mexicana</i>	Black tea	Chakravorty et al. (2016)
	<i>kudriavzevii</i>	Black tea	Tsilo et al. (2021)
<i>Rhodotorula</i>	<i>muliginosa</i>	Black tea	Teoh et al. (2004)
<i>Saccharomyces</i>	<i>cerevisiae</i>	Green and black tea	(Al-Mohammadi et al., 2021; Chakravorty et al., 2016; Coton et al., 2017; Fabricio et al., 2022; Góes-Neto et al., 2021; Landis et al., 2022; Tran et al., 2021, 2022)
	<i>uvorum</i>	Black tea	Coton et al. (2017)
<i>Saccharomycopsis</i>	<i>fibuligera</i>	Black tea	Chakravorty et al. (2016)
<i>Saccharomycodes</i>	<i>ludwigii</i>	Green tea	Landis et al. (2022)
<i>Schizosaccharomyces</i>	<i>pombe</i>	Green and Black tea	(Al-Mohammadi et al., 2021; Góes-Neto et al., 2021; Landis et al., 2022; Teoh et al., 2004; Villarreal-Soto et al., 2020)
<i>Sporopachydermia</i>	<i>lactativora</i>	Black tea	Chakravorty et al. (2016)
<i>Starmera</i>	<i>amethionina</i>	Black tea	Chakravorty et al. (2016)
	<i>caribaea</i>	Black tea	Chakravorty et al. (2016)
<i>Torulospora</i>	<i>delbreuckii</i>	Black tea	Teoh et al. (2004)
	<i>microellipsoides</i>	Green tea	Coton et al. (2017)
<i>Yarrowia</i>	<i>lipolytica</i>	Black tea	Reva et al. (2015)
<i>Zygosaccharomyces</i>	spp.	Green and black tea, biofilm, lemon verbena, mallow, wild rose, peppermint	(Arkan et al., 2020; Grassi et al., 2022; Marsh et al., 2014; Watawana et al., 2016)
	<i>bailii</i>	Green and black tea	(Arkan et al., 2020; Landis et al., 2022; Mukadam et al., 2016; Podolich et al., 2017; Teoh et al., 2004)
	<i>mellis</i>	Green tea	Landis et al. (2022)
	<i>parabailii</i>		Gaggia et al., 2018; Landis et al., 2022

Table 2 (continued)

GENUS	SPECIES	TYPE OF KOMBUCHA	REFERENCES
	<i>rouxii</i>	Green tea	Landis et al. (2022)
<i>Zygorulasporea</i>	<i>florentina</i>	Black and green tea	Coton et al. (2017)
<i>Zygowillipsis</i>	<i>californica</i>	Black tea	Chakravorty et al. (2016)

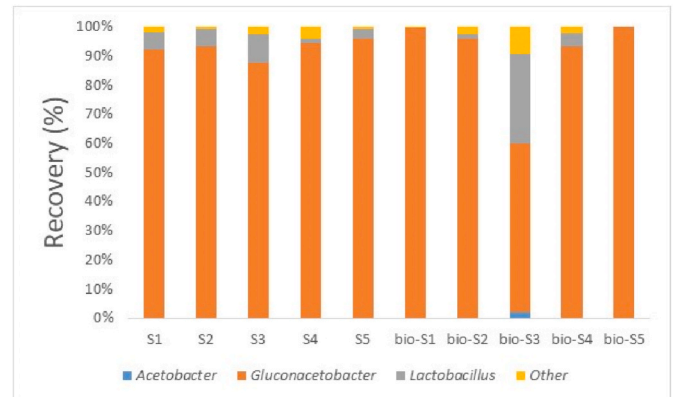


Fig. 3. Bacterial biota of kombucha. Data from Marsh et al. (2014). S1, S2, S3, S4 and S5, kombucha samples from Country 1, Country 2, Country 3, Country 4 and Country 5. bio-S1, bio-S2, bio-S3, bio-S4 and bio-S5, SCOBY from Country 1, Country 2, Country 3, Country 4 and Country 5.

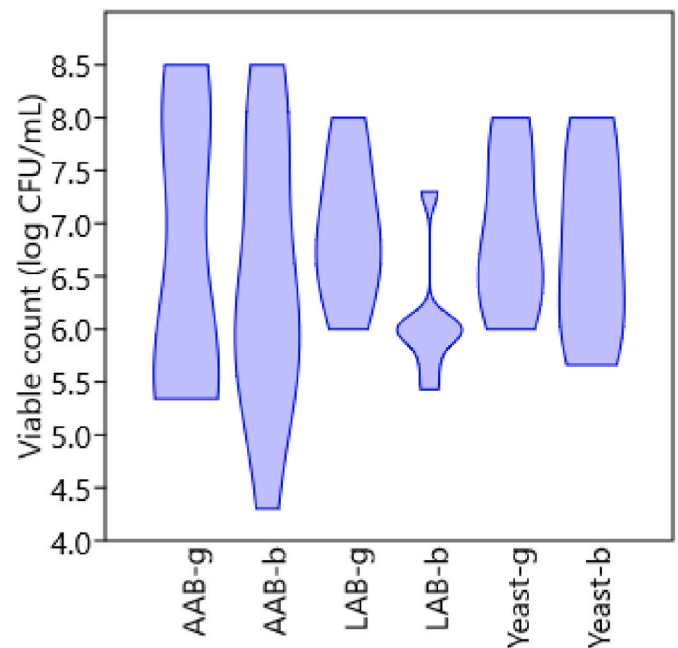


Fig. 4. Violin plot on the viable count of some microbial groups; AAB-b and AAB-g, acetic acid bacteria from black or green tea kombucha; LAB-b and LAB-g, lactic acid bacteria from black or green tea kombucha; Yeast-b and Yeast-g, yeasts in kombucha from green or black tea. Data from various bibliographic sources.

whether it is a probiotic drink or not.

According to the guidelines and amendment on probiotic definition, fermented foods with unknown or not characterized microbial consortia cannot be labeled as “probiotic” (Hill et al., 2014), although many recent

papers and reviews on kombucha use this definition (Selvaraj & Gurusurthy, 2023; Vargas et al., 2021). Due to the high biodiversity of kombucha, it is reasonable that potential probiotic strains could be isolated, identified, and characterized. However, according to the requirements set by different Regulatory Agencies (at least in EU), the use of the term “probiotic” is misleading and incorrect.

Possible probiotic strains could be isolated in kombucha from the species *Lacticaseibacillus casei*, *Lb. delbrueckii*, *Lactiplantibacillus plantarum*, *Lb. acidophilus*, *S. cerevisiae*, *Schizo. pombe*, *G. oxydans*, *Bif. bifidum*, and *Bif. longum*, among others, as shown in Table 2.

Bogdan et al. (2018) isolated a strain of *Pediococcus pentosaceus*, able to survive the harsh conditions of gut, to produce bacteriocins, as well as to adhere to intestinal cell lines (Utoiu et al., 2018), to exert antioxidant and antimicrobial activities (Diguță et al., 2020).

Pei et al. (2020) isolated and characterized a strain of *Lpb. plantarum* producing a bacteriocin, which increased cell membrane permeability, causing potassium ion release, and inhibits the formation of biofilms.

Potential probiotic strains were also found among AAB; Wang et al. (2014) identified a strain exerting hepatoprotective effects and identified it as *Gluconacetobacter* sp.; moreover, they also identified the compound responsible of this health-promoting effect, that is DSL.

6. Antimicrobial properties of kombucha

Due to the presence of various organic acids, high polyphenol content and LAB, the importance of kombucha as a natural antimicrobial source is increasing and has therefore been widely studied in recent years (Kaewkod et al., 2019). Pei et al. (2020) reported that SGL10 bacteriocin produced by *Lpb. plantarum* SLG10 isolated from kombucha acts on Gram positive and Gram negative bacteria. Another study has shown the antimicrobial effects of kombucha prepared using green, oolong, and black tea on *Escherichia coli*, *E. coli* O157:H7 DMST 12743, *Shigella dysenteriae* DMST 1511, *Salmonella* Typhi DMST 22842, and *Vibrio cholerae* (Kaewkod et al., 2019).

In general, essential oils' antimicrobial activity is attributed to several small terpenoid and phenolic compounds (such as thymol, carvacrol, eugenol) (Battikh et al., 2013). Bhattacharya et al. (2016, 2018) compared the antimicrobial effects of polyphenol content of black tea and kombucha on enterotoxigenic *E. coli*, *V. cholerae*, *Sh. flexneri*, and *Salmonella* Typhimurium. They found that the antimicrobial effect was related to some key-compounds (isorhamnetin, and catechin) able to cause an increase in membrane permeability.

In another study, unfermented tea and acetic acid were used as control, and kombucha was found to have antimicrobial effects on *Staphylococcus aureus*, *Sh. sonnei*, *E. coli*, *Aeromonas hydrophila*, *Yersinia enterocolitica*, *Pseudomonas aeruginosa*, *Enterobacter cloacae*, *Staph. epidermidis*, *Campylobacter jejuni*, *Salmonella* Enteritidis, *Salmonella* Typhimurium, *Bacillus cereus*, *Helicobacter pylori*, and *Listeria monocytogenes*; only *Z. bailii* was not affected (Sreeramulu et al., 2000).

Battikh et al. (2012) evaluate the antimicrobial activity of kombucha produced from thyme, lemon verbena, rosemary, fennel, and peppermint, and black tea. *Staph. epidermidis*, *Staph. aureus*, *Micrococcus lysodeikticus*, *E. coli*, *Ps. aeruginosa*, *Salmonella* Typhimurium, and *L. monocytogenes* were found to be sensitive to black tea, lemon verbena, and peppermint kombucha.

Greenwalt et al. (1998) reported that kombucha prepared with different amounts of green and black tea showed antimicrobial effects against *Staph. aureus*, *E. coli*, *Salmonella* Typhimurium, *B. cereus*, *Agrobacterium tumefaciens*, even at the lowest amount of tea. In contrast, no effect was observed against *Candida albicans*.

Diguță et al. (2020) showed that two probiotic strains belonging to the specie *P. pentosaceus* and *P. acidilactici* had high inhibitory activity against pathogenic bacteria such as *Salmonella* Typhimurium, *L. monocytogenes*, *L. ivanovii*, *B. cereus*, *Proteus hauseri*, and methicillin-resistant *Staph. aureus*.

7. Conclusions

Kombucha represents a high source of biodiversity, and is a promising raw material for the isolation and characterization of functional microorganisms; in addition, it is also a source of bioactive compounds, with health-promoting effects and antimicrobial properties towards a wide variety of pathogens (*Salmonella* sp., *L. monocytogenes*, *Staphylococcus* spp., *C. albicans*, among others).

The microbiota of kombucha is composed of five main bacterial phyla (Actinobacteria, Bacteroidetes, Deinococcus-Thermus, Firmicutes, and Proteobacteria), and AAB, mainly *Gluconacetobacter*, *Acetobacter*, *Komagataebacter*, and *Gluconobacter*, represent the most important group, while LAB are usually recovered at low frequencies. Yeast biota is also characterized by a high degree of biodiversity and *Zygosaccharomyces* is the most important genus.

There is still a debate on the “probiotic status” of kombucha, but according to authors' experience postbiotic definition could be more suitable.

Due to the complex biota of SCOBY, and the interactions occurring among the different taxa there living, kombucha could be a valuable model system to understand the importance of biodiversity to design new processes and products, thus improving fermentation paths and procedures.

This paper has contributed to the debate on the potentialities and microbiology of kombucha and has pointed out future perspectives and open questions.

Author contribution

All authors conceived the research; Antonio Bevilacqua, and Hayrunisa İçen performed literature search; Antonio Bevilacqua, performed statistics; Antonio Bevilacqua and Hayrunisa İçen wrote the first draft of the paper; Maria Rosaria Corbo, Milena Sinigaglia, and Burcu Irem Omurtag Korkmaz revised the manuscript; Maria Rosaria Corbo, and Milena Sinigaglia funded the research.

Funding declaration

Hayrunisa İçen received a grant in the framework of Erasmus+ KA131 Student Traineeship Mobility for her research visit at the Department of the Science of Agriculture, Food, Natural Resources and Engineering (Project number: 2021-1-TR01-KA131-HED-000005681).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

References

- Abou-Taleb, K., Ebeed, N., Soheir, S., Saad Abd El-salam, S., & Amin, S. (2017). Antimicrobial and antiproliferative, pro-apoptotic actions of kombucha fermented solutions against colon and heptao cancer cell lines. *World Journal of Pharmaceutical and Life Sciences*, 3, 120–132.
- Akbarirad, H., Mazaheri Assadi, M., & Pourahmad, R. (2017). Employing of the different fruit juices substrates in vinegar kombucha preparation. *Current Nutrition & Food Science*, 13, 303–307. <https://doi.org/10.2174/1573401313666170214165641>
- Al-Mohammadi, A. R., Ismaiel, A. A., Ibrahim, R. A., Moustafa, A. H., Abou Zeid, A., & Enan, G. (2021). Chemical constitution and antimicrobial activity of kombucha fermented beverage. *Molecules*, 26(16). <https://doi.org/10.3390/molecules26165026>. Article 16.
- Alderson, H., Liu, C., Mehta, A., Gala, H. S., Mazive, N. R., Chen, Y., Zhang, Y., Wang, S., & Serventi, L. (2021). Sensory profile of kombucha brewed with New Zealand

- ingredients by focus group and word clouds. *Fermentation*, 7(3). <https://doi.org/10.3390/fermentation7030100>. Article 3.
- Antolak, H., Piechota, D., & Kucharska, A. (2021). Kombucha tea—a double power of bioactive compounds from tea and symbiotic culture of bacteria and yeasts (SCOBY). *Antioxidants*, 10(10), 1541. <https://doi.org/10.3390/antiox10101541>
- Arıkan, M., Mitchell, A. L., Finn, R. D., & Gürel, F. (2020). Microbial composition of kombucha determined using amplicon sequencing and shotgun metagenomics. *Journal of Food Science*, 85(2), 455–464. <https://doi.org/10.1111/1750-3841.14992>
- Battikh, H., Bakhrouf, A., & Ammar, E. (2012). Antimicrobial effect of kombucha analogues. *LWT - Food Science and Technology*, 47(1), 71–77. <https://doi.org/10.1016/j.lwt.2011.12.033>
- Battikh, H., Chaieb, K., Bakhrouf, A., & Ammar, E. (2013). Antibacterial and antifungal activities of black and green kombucha teas. *Journal of Food Biochemistry*, 37(2), 231–236. <https://doi.org/10.1111/j.1745-4514.2011.00629.x>
- Bauer-Petrovska, B., & Petrushevska-Tozi, L. (2000). Mineral and water soluble vitamin content in the kombucha drink. *International Journal of Food Science and Technology*, 35(2), 201–205. <https://doi.org/10.1046/j.1365-2621.2000.00342.x>
- Bhattacharya, D., Bhattacharya, S., Patra, M. M., Chakravorty, S., Sarkar, S., Chakraborty, W., Koley, H., & Gachhui, R. (2016). Antibacterial activity of polyphenolic fraction of kombucha against enteric bacterial pathogens. *Current Microbiology*, 73(6), 885–896. <https://doi.org/10.1007/s00284-016-1136-3>
- Bhattacharya, S., Gachhui, R., & Sil, P. C. (2013). Effect of kombucha, a fermented black tea in attenuating oxidative stress mediated tissue damage in alloxan induced diabetic rats. *Food and Chemical Toxicology*, 60, 328–340. <https://doi.org/10.1016/j.fct.2013.07.051>
- Bhattacharya, D., Ghosh, D., Bhattacharya, S., Sarkar, S., Karmakar, P., Koley, H., & Gachhui, R. (2018). Antibacterial activity of polyphenolic fraction of kombucha against *Vibrio cholerae*: Targeting cell membrane. *Letters in Applied Microbiology*, 66(2), 145–152. <https://doi.org/10.1111/lam.12829>
- Bogdan, M., Justine, S., Filofeia, D. C., Petruța, C. C., Gabriela, L., Roxana, U. E., & Florentina, M. (2018). Lactic acid bacteria strains isolated from kombucha with potential probiotic effect. *Romanian Biotechnological Letters*, 23(3).
- Cetojevic-Simin, D. D., Bogdanovic, G. M., Cvetkovic, D. D., & Velicanski, A. S. (2008). Antiproliferative and antimicrobial activity of traditional kombucha and *Satureja montana* L. kombucha. *Journal of BUON*, 13, 395–401.
- Chakravorty, S., Bhattacharya, S., Chatzinotas, A., Chakraborty, W., Bhattacharya, D., & Gachhui, R. (2016). Kombucha tea fermentation: Microbial and biochemical dynamics. *International Journal of Food Microbiology*, 220, 63–72. <https://doi.org/10.1016/j.ijfoodmicro.2015.12.015>
- Coton, M., Pawtowski, A., Taminiau, B., Burgaud, G., Deniel, F., Coulloume-Labarthe, L., Fall, A., Daube, G., & Coton, E. (2017). Unraveling microbial ecology of industrial-scale kombucha fermentations by metabarcoding and culture-based methods. *FEMS Microbiology Ecology*, 93(5). <https://doi.org/10.1093/femsec/fix048>
- De Filippis, F., Troise, A. D., Vitaglione, P., & Ercolini, D. (2018). Different temperatures select distinctive acetic acid bacteria species and promotes organic acids production during kombucha tea fermentation. *Food Microbiology*, 73, 11–16. <https://doi.org/10.1016/j.fm.2018.01.008>
- Diez-Ozaeta, I., & Astiazaran, O. J. (2022). Recent advances in kombucha tea: Microbial consortium, chemical parameters, health implications and biocellulose production. *International Journal of Food Microbiology*, 377, Article 109783. <https://doi.org/10.1016/j.ijfoodmicro.2022.109783>
- Diguță, C. F., Nițoi, G. D., Matei, F., Luță, G., & Cornea, C. P. (2020). The biotechnological potential of *Pediococcus* spp. isolated from kombucha microbial consortium. *Foods*, 9(12). <https://doi.org/10.3390/foods9121780>. Article 12.
- Dutta, D., & Gachhui, R. (2006). Novel nitrogen-fixing *Acetobacter nitrogenifigens* sp. Nov., isolated from kombucha tea. *International Journal of Systematic and Evolutionary Microbiology*, 56(8), 1899–1903. <https://doi.org/10.1099/ijs.0.64101-0>
- Emiljanowicz, K. E., & Malinowska-Pańczyk, E. (2020). Kombucha from alternative raw materials – the review. *Critical Reviews in Food Science and Nutrition*, 60(19), 3185–3194. <https://doi.org/10.1080/10408398.2019.1679714>
- Fabricio, M. F., Mann, M. B., Kothe, C. I., Frazzon, J., Tischer, B., Flores, S. H., & Ayub, M. A. Z. (2022). Effect of freeze-dried kombucha culture on microbial composition and assessment of metabolic dynamics during fermentation. *Food Microbiology*, 101, Article 103889. <https://doi.org/10.1016/j.fm.2021.103889>
- Fu, C., Yan, F., Cao, Z., Xie, F., & Lin, J. (2014). Antioxidant activities of kombucha prepared from three different substrates and changes in content of probiotics during storage. *Food Science and Technology*, 34, 123–126. <https://doi.org/10.1590/S0101-20612014005000012>
- Gaggia, F., Baffoni, L., Galiano, M., Nielsen, D. S., Jakobsen, R. R., Castro-Mejía, J. L., Bosi, S., Truzzi, F., Musumeci, F., Dinelli, G., & Di Gioia, D. (2018). Kombucha beverage from green, black and rooibos teas: A comparative study looking at microbiology, chemistry and antioxidant activity. *Nutrients*, 11(1), 1. <https://doi.org/10.3390/nu11010001>
- Góes-Neto, A., Kukharenko, O., Orlovskaya, I., Podolich, O., Imchen, M., Kumavath, R., Kato, R. B., de Carvalho, D. S., Tiwari, S., Brenig, B., Azevedo, V., Reva, O., de Vera, J. P. P., Kozyrovska, N., & Barh, D. (2021). Shotgun metagenomic analysis of kombucha mutualistic community exposed to Mars-like environment outside the International Space Station. *Environmental Microbiology*, 23(7), 3727–3742. <https://doi.org/10.1111/1462-2920.15405>
- Grassi, A., Cristani, C., Palla, M., Di Giorgi, R., Giovannetti, M., & Agnolucci, M. (2022). Storage time and temperature affect microbial dynamics of yeasts and acetic acid bacteria in a kombucha beverage. *International Journal of Food Microbiology*, 382, Article 109934. <https://doi.org/10.1016/j.ijfoodmicro.2022.109934>
- Greenwalt, C. J., Ledford, R. A., & Steinkraus, K. (1998). Determination and characterization of the antimicrobial activity of the fermented tea kombucha. *LWT - Food Science and Technology*, 31(3), 291–296. <https://doi.org/10.1006/food.1997.0354>
- Harrison, K., & Curtin, C. (2021). Microbial composition of SCOBY starter cultures used by commercial kombucha brewers in North America. *Microorganisms*, 9(5). <https://doi.org/10.3390/microorganisms9051060>. Article 5.
- Hill, C., Guarner, F., Reid, G., Gibson, G. R., Merenstein, D. J., Pot, B., Morelli, L., Canani, R. B., Flint, H. J., Salminen, S., Calder, P. C., & Sanders, M. E. (2014). The International Scientific Association for Probiotics and Prebiotics consensus statement on the scope and appropriate use of the term probiotic. *Nature Reviews Gastroenterology & Hepatology*, 11(8). <https://doi.org/10.1038/nrgastro.2014.66>. Article 8.
- Ivanišová, E., Meňhartová, K., Terentjeva, M., Godočíková, L., Árvay, J., & Kačániová, M. (2019). Kombucha tea beverage: Microbiological characteristic, antioxidant activity, and phytochemical composition. *Acta Alimentaria*, 48(3), 324–331. <https://doi.org/10.1556/066.2019.48.3.7>
- Jakubczyk, K., Kalduniska, J., Kochman, J., & Janda, K. (2020). Chemical profile and antioxidant activity of the kombucha beverage derived from white, green, black and red tea. *Antioxidants*, 9(5), 447. <https://doi.org/10.3390/antiox9050447>
- Jayabalan, R., Malbaša, R. V., Lončar, E. S., Vitas, J. S., & Sathishkumar, M. (2014). A review on kombucha tea—microbiology, composition, fermentation, beneficial effects, toxicity, and tea fungus. *Comprehensive Reviews in Food Science and Food Safety*, 13(4), 538–550. <https://doi.org/10.1111/1541-4337.12073>
- Jayabalan, R., Malini, K., Sathishkumar, M., Swaminathan, K., & Yun, S. E. (2010). Biochemical characteristics of tea fungus produced during kombucha fermentation. *Food Science and Biotechnology*, 19(3), 843–847. <https://doi.org/10.1007/s10068-010-0119-6>
- Kaashyap, M., Cohen, M., & Mantri, N. (2021). Microbial diversity and characteristics of kombucha as revealed by metagenomic and physicochemical analysis. *Nutrients*, 13(12). <https://doi.org/10.3390/nu13124446>. Article 12.
- Kaewkod, T., Bovonsombut, S., & Tragoolpua, Y. (2019). Efficacy of kombucha obtained from green, oolong, and black teas on inhibition of pathogenic bacteria, antioxidant, and toxicity on colorectal cancer cell line. *Microorganisms*, 7(12). <https://doi.org/10.3390/microorganisms7120700>. Article 12.
- Kayisoglu, S., & Coskun, F. (2020). Determination of physical and chemical properties of kombucha teas prepared with different herbal teas. *Food Science and Technology*, 41, 393–397. <https://doi.org/10.1590/1517-8720>
- Kitwetcharoen, H., Phung, L. T., Klanrit, P., Thanonkeo, S., Tippayawat, P., Yamada, M., & Thanonkeo, P. (2023). Kombucha healthy drink—recent advances in production, chemical composition and health benefits. *Fermentation*, 9(1). <https://doi.org/10.3390/fermentation9010048>. Article 1.
- Klawpiyapamornkun, T., Uttarotai, T., Wangkarn, S., Sirisa-ard, P., Kiatkarun, S., Tragoolpua, Y., & Bovonsombut, S. (2023). Enhancing the chemical composition of kombucha fermentation by adding Indian gooseberry as a substrate. *Fermentation*, 9(3). <https://doi.org/10.3390/fermentation9030291>. Article 3.
- Kruk, M., Trzaskowska, M., Ścibisz, I., & Pokorski, P. (2021). Application of the “SCOBY” and kombucha tea for the production of fermented milk drinks. *Microorganisms*, 9(1). <https://doi.org/10.3390/microorganisms9010123>. Article 1.
- La Torre, C., Fazio, A., Caputo, P., Plastina, P., Caroleo, M. C., Cannataro, R., & Cione, E. (2021). Effects of long-term storage on radical scavenging properties and phenolic content of kombucha from black tea. *Molecules*, 26(18). <https://doi.org/10.3390/molecules26185474>. Article 18.
- Landis, E. A., Fogarty, E., Edwards, J. C., Popa, O., Eren, A. M., & Wolfe, B. E. (2022). Microbial diversity and interaction specificity in kombucha tea fermentations. *mSystems*, 7(3), Article e00157. <https://doi.org/10.1128/mSystems.00157-22>. -22.
- Lazzaroli, C., Sordini, B., Daidone, L., Veneziani, G., Esposto, S., Urbani, S., Selvaggini, R., Servili, M., & Taticchi, A. (2023). Recovery and valorization of food industry by-products through the application of *Olea europaea* L. leaves in kombucha tea manufacturing. *Food Bioscience*, 53, Article 102551. <https://doi.org/10.1016/j.fbio.2023.102551>
- Lee, I., Barh, D., Podolich, O., Brenig, B., Tiwari, S., Azevedo, V., Góes-Neto, A., Reva, O., Kozyrovska, N., de Vera, J.-P., & Kim, B.-S. (2021). Metagenome-assembled genome sequences obtained from a reactivated kombucha microbial community exposed to a Mars-like environment outside the International Space Station. *Microbiology Resource Announcements*, 10(36). <https://doi.org/10.1128/mra.00549-21>. 10.1128/mra.00549-21.
- Lee, K. R., Jo, K., Ra, K. S., Suh, H. J., & Hong, K. B. (2021). Kombucha fermentation using commercial kombucha pellicle and culture broth as starter. *Food Science and Technology*, 42, Article e70020. <https://doi.org/10.1590/1517-8720>
- Lončar, E., Djurić, M., Malbaša, R., Kolarov, L. J., & Klačnja, M. (2006). Influence of working conditions upon kombucha conducted fermentation of black tea. *Food and Bioprocess Technology*, 84(3), 186–192. <https://doi.org/10.1205/fbp.04306>
- Malbaša, R. V., Lončar, E. S., Vitas, J. S., & Čanadanović-Brunet, J. M. (2011). Influence of starter cultures on the antioxidant activity of kombucha beverage. *Food Chemistry*, 127(4), 1727–1731. <https://doi.org/10.1016/j.foodchem.2011.02.048>
- Marsh, A. J., O’Sullivan, O., Hill, C., Ross, R. P., & Cotter, P. D. (2014). Sequence-based analysis of the bacterial and fungal compositions of multiple kombucha (tea fungus) samples. *Food Microbiology*, 38, 171–178. <https://doi.org/10.1016/j.fm.2013.09.003>
- Martínez Leal, J., Valenzuela Suárez, L., Jayabalan, R., Huerta Oros, J., & Escalante-Aburto, A. (2018). A review on health benefits of kombucha nutritional compounds and metabolites. *CyTA - Journal of Food*, 16(1), 390–399. <https://doi.org/10.1080/19476337.2017.1410499>
- Martínez-Leal, J., Ponce-García, N., & Escalante-Aburto, A. (2020). Recent evidence of the beneficial effects associated with glucuronic acid contained in kombucha beverages. *Current Nutrition Reports*, 9, 163–170. <https://doi.org/10.1007/s13668-020-00312-6>

- Miranda, B., Lawton, N. M., Tachibana, S. R., Swartz, N. A., & Hall, W. P. (2016). Titration and HPLC characterization of kombucha fermentation: A laboratory experiment in food analysis. *Journal of Chemical Education*, 93(10), 1770–1775. <https://doi.org/10.1021/acs.jchemed.6b00329>
- Moreira, G. V., Araujo, L. C. C., Murata, G. M., Matos, S. L., & Carvalho, C. R. O. (2022). Kombucha tea improves glucose tolerance and reduces hepatic steatosis in obese mice. *Biomedicine & Pharmacotherapy = Biomedicine & Pharmacotherapie*, 155, Article 113660. <https://doi.org/10.1016/j.biopha.2022.113660>
- Mousavi, S. M., Hashemi, S. A., Zarei, M., Gholami, A., Lai, C. W., Chiang, W. H., Omidifar, N., Bahrani, S., & Mazraedoost, S. (2020). Recent progress in chemical composition, production, and pharmaceutical effects of kombucha beverage: A complementary and alternative medicine. *Evidence-based Complementary and Alternative Medicine: ECAM*, Article 4397543. <https://doi.org/10.1155/2020/4397543>, 2020.
- Mukadam, T. A., Punjabi, K., Deshpande, S. D., Vaidya, S. P., & Chowdhary, A. S. (2016). Isolation and characterization of bacteria and yeast from kombucha tea. *International Journal of Current Microbiology and Applied Sciences*, 5(6), 32–41. <https://doi.org/10.20546/ijcmas.2016.506.004>
- Neffe-Skocińska, K., Sionek, B., Scibisz, I., & Kolożyn-Krajewska, D. (2017). Acid contents and the effect of fermentation condition of kombucha tea beverages on physicochemical, microbiological and sensory properties. *CyTA - Journal of Food*, 15(4), 601–607. <https://doi.org/10.1080/19476337.2017.1321588>
- Nguyen, N. K., Dong, N. T. N., Nguyen, H. T., & Le, P. H. (2015). Lactic acid bacteria: Promising supplements for enhancing the biological activities of kombucha. *SpringerPlus*, 4(1), 91. <https://doi.org/10.1186/s40064-015-0872-3>
- Nguyen, N. K., Nguyen, P. B., Nguyen, H. T., & Le, P. H. (2015). Screening the optimal ratio of symbiosis between isolated yeast and acetic acid bacteria strain from traditional kombucha for high-level production of glucuronic acid. *LWT - Food Science and Technology*, 64(2), 1149–1155. <https://doi.org/10.1016/j.lwt.2015.07.018>
- Özdemir, N., & Çon, A. H. (2017). Kombucha and health. *Journal of Health Science*, 5(5). <https://doi.org/10.17265/2328-7136/2017.05.005>
- Pei, J., Jin, W., Abd El-Aty, A. M., Baranenko, D. A., Gou, X., Zhang, H., Geng, J., Jiang, L., Chen, D., & Yue, T. (2020). Isolation, purification, and structural identification of a new bacteriocin made by *Lactobacillus plantarum* found in conventional kombucha. *Food Control*, 110, Article 106923. <https://doi.org/10.1016/j.foodcont.2019.106923>
- Permatasari, H. K., Firani, N. K., Prijadi, B., Irnandi, D. F., Riawan, W., Yusuf, M., Amar, N., Chandra, L. A., Yusuf, V. M., Subali, A. D., & Nurkolis, F. (2022). Kombucha drink enriched with sea grapes (*Caulerpa racemosa*) as potential functional beverage to contrast obesity: An in vivo and in vitro approach. *Clinical Nutrition ESPEN*, 49, 232–240. <https://doi.org/10.1016/j.clnesp.2022.04.015>
- Phung, L. T., Kitwetcharoen, H., Chamnipa, N., Boonchot, N., Thanonkeo, S., Tippayawat, P., Klanrit, P., Yamada, M., & Thanonkeo, P. (2023). Changes in the chemical compositions and biological properties of kombucha beverages made from black teas and pineapple peels and cores. *Scientific Reports*, 13(1). <https://doi.org/10.1038/s41598-023-34954-7>, Article 1.
- Podolich, O., Zaets, I. E., Kukharenko, O., Orlovskaya, I., Reva, O., Khirunenko, L., Sosnin, M., Haidak, A., Shpylova, S., Rabbow, E., Skoryk, M., Kremenskoy, M., Demets, R., Kozyrovska, N., & Vera, J. P. (2017). Kombucha multimicrobial community under simulated spaceflight and Martian conditions. *Astrobiology*, 17, 459–469. <https://doi.org/10.1089/ast.2016.1480>
- Pure, A. E., & Pure, M. E. (2016). Antioxidant and antibacterial activity of kombucha beverages prepared using banana peel, common nettles and black tea infusions. *Applied Food Biotechnology*, 3, 125–130. <https://doi.org/10.22037/afb.v3i2.11138>
- Rahmani, R., Beaufort, S., Villarreal-Soto, S. A., Taillandier, P., Bouajila, J., & Deboutba, M. (2019). Kombucha fermentation of African mustard (*Brassica tournefortii*) leaves: Chemical composition and bioactivity. *Food Bioscience*, 30, Article 100414. <https://doi.org/10.1016/j.fbio.2019.100414>
- Ramírez Tapias, Y. A., Di Monte, M. V., Peltzer, M. A., & Salvay, A. G. (2022). Bacterial cellulose films production by kombucha symbiotic community cultured on different herbal infusions. *Food Chemistry*, 372, Article 131346. <https://doi.org/10.1016/j.foodchem.2021.131346>
- Reva, O. N., Zaets, I. E., Ovcharenko, L. P., Kukharenko, O. E., Shpylova, S. P., Podolich, O. V., de Vera, J.-P., & Kozyrovska, N. O. (2015). Metabarcoding of the kombucha microbial community grown in different microenvironments. *AMB Express*, 5(1), 35. <https://doi.org/10.1186/s13568-015-0124-5>
- Selvaraj, S., & Gurumurthy, K. (2023). An overview of probiotic health booster-kombucha tea. *Chinese Herbal Medicines*, 15(1), 27–32. <https://doi.org/10.1016/j.chmed.2022.06.010>
- Semjonovs, P., Rukliša, M., Paegle, L., Saka, M., Treimane, R., Skute, M., Rozenberga, L., Vikele, L., Sabovics, M., & Cleeenwerck, I. (2017). Cellulose synthesis by *Komagataeibacter rhaeticus* strain P 1463 isolated from kombucha. *Applied Microbiology and Biotechnology*, 101(3), 1003–1012. <https://doi.org/10.1007/s00253-016-7761-8>
- Shahbazi, H., Hashemi Gahrue, H., Golmakani, M., Eskandari, M. H., & Movahedi, M. (2018). Effect of medicinal plant type and concentration on physicochemical, antioxidant, antimicrobial, and sensorial properties of kombucha. *Food Science and Nutrition*, 6(8), 2568–2577. <https://doi.org/10.1002/fsn3.873>
- Sievers, M., Lanini, C., Weber, A., Schuler-Schmid, U., & Teuber, M. (1995). Microbiology and fermentation balance in a kombucha beverage obtained from a tea fungus fermentation. *Systematic & Applied Microbiology*, 18(4), 590–594. [https://doi.org/10.1016/S0723-2020\(11\)80420-0](https://doi.org/10.1016/S0723-2020(11)80420-0)
- Sknepnek, A., Pantić, M., Matijašević, D., Miletić, D., Lević, S., Nedović, V., & Nikšić, M. (2018). Novel kombucha beverage from lingzhi or reishi medicinal mushroom, *Ganoderma lucidum*, with antibacterial and antioxidant effects. *International Journal of Medicinal Mushrooms*, 20(3), 243–258. <https://doi.org/10.1615/IntJMedMushrooms.2018025833>
- Sreeramulu, G., Zhu, Y., & Knol, W. (2000). Kombucha fermentation and its antimicrobial activity. *Journal of Agricultural and Food Chemistry*, 48(6), 2589–2594. <https://doi.org/10.1021/jf991333m>
- Tamer, C., Temel, Ş., Suna, S., Karabacak, A., Özcan, T., Ersan, L., Kaya, B., & Çopur, Ö. (2021). Evaluation of bioaccessibility and functional properties of kombucha beverages fortified with different medicinal plant extracts. *Turkish Journal of Agriculture and Forestry*, 45(1), 13–32. <https://doi.org/10.3906/tar-2003-75>
- Tan, W. C., Muhialdin, B. J., & Meor Hussin, A. S. (2020). Influence of storage conditions on the quality, metabolites, and biological activity of soursop (*Annona muricata* L.) kombucha. *Frontiers in Microbiology*, 11, Article 603481. <https://www.frontiersin.org/articles/10.3389/fmicb.2020.603481>
- Tanticharakunsiri, W., Mangmool, S., Wongsariya, K., & Ochaikul, D. (2021). Characteristics and upregulation of antioxidant enzymes of kitchen mint and oolong tea kombucha beverages. *Journal of Food Biochemistry*, 45(1), Article e13574. <https://doi.org/10.1111/jfbc.13574>
- Teoh, A. L., Heard, G., & Cox, J. (2004). Yeast ecology of kombucha fermentation. *International Journal of Food Microbiology*, 95(2), 119–126. <https://doi.org/10.1016/j.ijfoodmicro.2003.12.020>
- Tran, T., Billet, K., Torres-Cobos, B., Vichi, S., Verdier, F., Martin, A., Alexandre, H., Grandvalet, C., & Tourdot-Maréchal, R. (2022). Use of a minimal microbial consortium to determine the origin of kombucha flavor. *Frontiers in Microbiology*, 13, Article 836617. <https://doi.org/10.3389/fmicb.2022.836617>
- Tran, T., Grandvalet, C., Verdier, F., Martin, A., Alexandre, H., & Tourdot-Maréchal, R. (2020). Microbiological and technological parameters impacting the chemical composition and sensory quality of kombucha. *Comprehensive Reviews in Food Science and Food Safety*, 19(4), 2050–2070. <https://doi.org/10.1111/1541-4337.12574>
- Tran, T., Grandvalet, C., Winckler, P., Verdier, F., Martin, A., Alexandre, H., & Tourdot-Maréchal, R. (2021). Shedding light on the formation and structure of kombucha biofilm using two-photon fluorescence microscopy. *Frontiers in Microbiology*, 12, Article 725379. <https://www.frontiersin.org/articles/10.3389/fmicb.2021.725379>
- Tsilos, P. H., Basson, A. K., Ntombela, Z. G., Maliehe, T. S., & Pullabhotla, R. V. S. R. (2021). Isolation and optimization of culture conditions of a bioflocculant-producing fungi from kombucha tea SCOBY. *Microbiology Research*, 12(4). <https://doi.org/10.3390/microbiolres12040070>, Article 4.
- Tu, C., Tang, S., Azi, F., Hu, W., & Dong, M. (2019). Use of kombucha consortium to transform soy whey into a novel functional beverage. *Journal of Functional Foods*, 52, 81–89. <https://doi.org/10.1016/j.jff.2018.10.024>
- Utoi, E., Matei, F., Toma, A., Diguta, C., Stefan, L., Mănoiu, S., Vrajmasu, V., Moraru, I., Oancea, A., Israel-Roming, F., Cornea, C. P., Constantinescu Aruxandei, D., Moraru, A., & Oancea, F. (2018). Bee collected pollen with enhanced health benefits, produced by fermentation with a kombucha consortium. *Nutrients*, 10, 1365. <https://doi.org/10.3390/nu10101365>
- Vargas, B. K., Fabricio, M. F., & Záchia Ayub, M. A. (2021). Health effects and probiotic and prebiotic potential of kombucha: A bibliometric and systematic review. *Food Bioscience*, 44, Article 101332. <https://doi.org/10.1016/j.fbio.2021.101332>
- Velicanski, A., Cvetkovi, D., & Markov, S. (2013). Characteristics of kombucha fermentation on medicinal herbs from Lamiaceae family. *Romanian Biotechnological Letters*, 18(1), 8034–8042.
- Villarreal-Soto, S. A., Beaufort, S., Bouajila, J., Souchard, J.-P., Renard, T., Rollan, S., & Taillandier, P. (2019). Impact of fermentation conditions on the production of bioactive compounds with anticancer, anti-inflammatory and antioxidant properties in kombucha tea extracts. *Process Biochemistry*, 83, 44–54. <https://doi.org/10.1016/j.procbio.2019.05.004>
- Villarreal-Soto, S. A., Bouajila, J., Pace, M., Leech, J., Cotter, P. D., Souchard, J. P., Taillandier, P., & Beaufort, S. (2020). Metabolome-microbiome signatures in the fermented beverage, Kombucha. *International Journal of Food Microbiology*, 333, Article 108778. <https://doi.org/10.1016/j.ijfoodmicro.2020.108778>
- Vitas, J. S., Cvetanović, A. D., Mašković, P. Z., Švarc-Gajić, J. V., & Malbasa, R. V. (2018). Chemical composition and biological activity of novel types of kombucha beverages with yarrow. *Journal of Functional Foods*, 44, 95–102. <https://doi.org/10.1016/j.jff.2018.02.019>
- Vitas, J., Vukmanovic, S., Cakarevic, J., Popovic, L., & Malbasa, R. (2020). Kombucha fermentation of six medicinal herbs: Chemical profile and biological activity. *Chemical Industry and Chemical Engineering Quarterly*, 26(2), 157–170. <https://doi.org/10.2298/CICEQ190708034V>
- Vohra, B. M., Fazry, S., Sairi, F., & Babul-Airannah, O. (2019). Effects of medium variation and fermentation time on the antioxidant and antimicrobial properties of kombucha. In *Malaysian Journal of Fundamental and applied sciences, special issue on international conference on agriculture, animal sciences and food technology 2018* (pp. 298–302). <https://doi.org/10.11113/mjfas.v15n2-1.1536>
- Wang, Y., Ji, B., Wu, W., Wang, R., Yang, Z., Zhang, D., & Tian, W. (2014). Hepatoprotective effects of kombucha tea: Identification of functional strains and quantification of functional components. *Journal of the Science of Food and Agriculture*, 94(2), 265–272. <https://doi.org/10.1002/jsfa.6245>
- Wang, X., Wang, D., Wang, H., Jiao, S., Wu, J., Hou, Y., Sun, J., & Yuan, J. (2022). Chemical profile and antioxidant capacity of kombucha tea by the pure cultured kombucha. *LWT-Food Science & Technology*, 168, Article 113931. <https://doi.org/10.1016/j.lwt.2022.113931>
- Watawana, M. I., Jayawardena, N., Gunawardhana, C. B., & Waisundara, V. Y. (2016). Enhancement of the antioxidant and starch hydrolase inhibitory activities of king coconut water (*Cocos nucifera* var. *aurantiaca*) by fermentation with kombucha 'tea fungus'. *International Journal of Food Science and Technology*, 51(2), 490–498. <https://doi.org/10.1111/ijfs.13006>

- Yang, J., Lagishetty, V., Kurnia, P., Henning, S. M., Ahdoot, A. I., & Jacobs, J. P. (2022). Microbial and chemical profiles of commercial kombucha products. *Nutrients*, *14*(3), 670. <https://doi.org/10.3390/nu14030670>
- Yıkımsı, S., & Tuğgüm, S. (2019). Evaluation of microbiological, physicochemical and sensorial properties of purple basil kombucha beverage. *Turkish Journal of Agriculture - Food Science and Technology*, *7*(9), 1321–1327. <https://doi.org/10.24925/turjaf.v7i9.1321-1327.2550>
- Zhou, D. D., Saimaiti, A., Luo, M., Huang, S. Y., Xiong, R. G., Shang, A., Gan, R. Y., & Li, H. B. (2022). Fermentation with tea residues enhances antioxidant activities and polyphenol contents in kombucha beverages. *Antioxidants*, *11*(1), 155. <https://doi.org/10.3390/antiox11010155>
- Ziska, R., & Agustina, A. (2019). Cytotoxic activity assay of n-hexane extract of *Solanum nigrum* L. fruits fermented by kombucha against MCF-7 breast cancer cell line. *Journal of Physics: Conference Series*, *1338*(1), Article 012027.