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Review

Lactic Acid Bacteria in Vinegar Fermentation: Diversity, Functionality and Health Benefits

Elahesadat Hosseini [1,2], Zenebe Tadesse Tsegay [3], Slim Smaoui [4] and Theodoros Varzakas [5,*]

[1] National Nutrition and Food Technology Research Institute, Faculty of Nutrition Sciences and Food Technology, Shahid Beheshti University of Medical Sciences, Tehran, Iran
[2] Department of Chemical Engineering, Payame Noor University, Tehran, Iran
[3] Department of Food Science and Post-Harvest Technology, College of Dryland Agriculture and Natural Resources, Mekelle University, Mekelle P.O. Box 231, Ethiopia
[4] Laboratory of Microbial and Enzymatic Biotechnologies and Biomolecules, Center of Biotechnology of Sfax (CBS), University of Sfax, Road of Sidi Mansour Km 6, P.O. Box 1177, Sfax 3018, Tunisia
[5] Department of Food Science and Technology, University of the Peloponnese, Antikalamos, 24100 Kalamata, Greece
* Correspondence: t.varzakas@uop.gr

Abstract: Lactic acid bacteria (LAB) play a pivotal role in vinegar fermentation, contributing significantly to its functional and sensory qualities. This review examines the microbial diversity of Lactic Acid Bacteria (LAB) in vinegar fermentation, focusing on their specific metabolic contributions and the bioactive compounds they produce, which contribute to vinegar's sensory and health benefits. Key bioactive components produced or enriched by LAB, such as organic acids, phenolic compounds, melanoidins, and tetramethylpyrazine, have demonstrated health benefits, including antibacterial, antioxidant, anti-inflammatory, and metabolic regulatory effects. These properties position vinegar as a promising functional food with potential health applications. The review also explores advancements in vinegar production, including modernized fermentation processes and optimized aging techniques, which enhance these beneficial compounds and ensure product consistency and safety. By examining the variety of LAB strains and the bioactive profiles of different vinegar types, this study highlights vinegar's value beyond a culinary product, as a potential therapeutic agent in human nutrition and health. The findings underscore vinegar's relevance not only in dietary and preventive healthcare but also as a potential functional food ingredient. Further research is needed to explore the mechanisms of action through which LAB contribute to vinegar's health benefits, particularly in areas like metabolic regulation, anti-inflammatory effects, and antioxidant properties.

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1. Introduction

Lactic acid bacteria (LAB) can be employed as probiotics, offering major health benefits [1]. They have been linked with dairy and non-dairy products lately due to the high demand for gluten-free and lactose-free products [2]. Vinegar constitutes one of the earliest culinary creations representing an ancient fermented food with a long history dating back to 2000 BCE [3]. Its sedative and curative properties make its application as a remedy unique with reports in the Bible [4]. It can be employed as a preservative, a flavor enhancer, but also as a cleaning agent for surfaces and utensils [5]. The natural fermentation of vinegar involves the presence of LAB [6].

LAB species, utilizing plants, cereals, fruits, whey, and honey as raw materials are usually introduced at the initial stage of vinegar fermentation [7]. Even at lower concentrations, LAB can be constant and/or dominate vinegar fermentation [8,9].

Vinegar harnesses antibacterial properties and fosters tissue repair and this is ascribed to the extracellular structure synthesized by *Acetobact*er species [10]. It has an antidiabetic effect which is due to the action of acetic acid as reported by the previous authors and a hypotensive effect is reported for red wine vinegar by inhibition of the renin-angiotensin system in rats [11]. It might also protect against oxidative stress-related injuries [12], also promoting anti-inflammatory and anti-cancer activities. Excretion of calcium works for acetate for the prevention of kidney stone formation [1], which can also reduce glucose blood levels by helping its conversion to glycogen [13]. Vinegar's consumption benefits are directly influenced by the bioactive compounds produced by LAB, such as those isolated from tangerine vinegar, which include organic acids, polyphenols, and melanoidins. These compounds are known for their antioxidant, anti-inflammatory, and metabolic-regulating properties, which are linked to the health benefits of vinegar [14]. On the other hand, some of the organic acids and bioactive components of vinegar (e.g., acetic acid, gallic acid, catechin, epicatechin, chlorogenic acid, caffeic acid, p-coumaric acid, and ferulic acid) [10], could play a crucial role in various physiological processes such as absorption of minerals by lowering the gastrointestinal pH [15].

This review aims to compile the overall microbial diversity of LAB in vinegar and identify vinegar's functional and bioactive compounds along with their health benefits making it a postbiotic supplement in human nutrition. We have searched the internet and databases such as Scopus, Science Direct, Researchgate with the keywords lactic acid bacteria, and fermentation, and vinegar, and health benefits, and diversity, or functionality.

2. Diversity and Application of LAB During Vinegar Fermentation

Vinegar fermentation involves a remarkable diversity of LAB, surpassing that of acetic acid bacteria (AAB). LAB encompass six genera and 26 species, with major genera including Lactobacillus, Pediococcus, Leuconostoc, and others. These species play distinct roles at various stages of fermentation, such as early fermentation, flavor development, and health-promoting compound production [16]. LAB are extensively present in various vinegar types including apple [17], rice [18,19], cereal [20,21], Shanxi-aged [8], Zhejiang rosy [6], Zhenjiang aromatic vinegar [22,23], Qishan [24], and Tianjin Duliu [25], Sichuan sun vinegar [26–28], rose vinegar [29], malt vinegar [30], persimmon vinegar [31], highlighting their significant role throughout the fermentation process [6]. The dominant genus, Lactobacillus, constitutes over 70% of the LAB population and includes key species such as L. plantarum, L. casei, L. acetotolerans, and L. fermentum [25]. Following closely, the Pediococcus genus predominantly features P. acidilactici and P. pentosaceus. Additionally, species such as *Weissella confusa*, *Lactococcus lactis*, *Leuconostoc mesenteroides*, and *Oenococcus* contribute to the complex microbial ecosystem during vinegar production [24]. The presence and dominance of different LAB genera vary across fermentation stages and vinegar types. For example, *Lactobacillus* is prevalent in most types except for rice and cereal vinegar [18,20]. Additionally, *Pediococcus and Lactococcus* are dominant in Shanxi-aged vinegar [8] and Daqu starter [32], while *Weissella* is common in Tianjin Duliu and Qishan vinegar [24,25]. *Leuconostoc* thrives in Qishan vinegar, and *Oenococcus* is associated with apple vinegar fermentation [33].

LAB typically dominate the early and middle stages of vinegar fermentation, often in symbiosis with yeasts such as Saccharomyces cerevisiae predominate the group ranging within 10^2–10^6 CFU/g with the total microbial population of vegetables and fruits ranging between 10^5 and 10^7 CFU/g and LAB, representing the minor part of the microbiota, ranging between 10^2 and 10^4 CFU/g [34], which provide essential amino acids and vitamins. In turn, LAB, particularly species such as *Lactobacillus plantarum*, *Lactobacillus acetotolerans*, and *Pediococcus acidilactici*, play a significant role in the early stages of fermentation. These species are responsible for lactic acid production, which lowers the pH of the fermentation medium. This process creates an optimal environment for the formation of polyphenols and melanoidins, compounds known for their antioxidant and anti-inflammatory properties [35]. For instance, during the initial 10–30 days of Zhejiang rosy vinegar fermentation, Lactobacillus is predominant; however, Acetobacter becomes more abundant during later stages [6].

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LAB abundance tends to decline as the fermentation process progresses into acetic acid fermentation (AAF) due to their low tolerance for acidic conditions [36]. Despite this, species such as L. acetotolerans and L. fermentum persist, demonstrating their adaptability to low pH environments [8,25].

Beyond their role in microbial dynamics, LAB play a critical part in improving the sensory characteristics and safety of vinegar [9]. They produce lactic acid, which lowers pH and imparts a fresh and mild sourness that balances the strong acidity of acetic acid [23,25]. LAB also generate volatile compounds like esters and aldehydes, contributing to fruity, creamy, and buttery flavors in vinegar, which enhance the sensory quality of the final product. Furthermore, melanoidins produced during fermentation are known for their antioxidant properties, which contribute to the health-promoting effects of vinegar, such as oxidative stress reduction [36,37]. For example; the key microorganisms responsible for the flavor of Zhenjiang aromatic vinegar (ZAV) include *Lactobacillus acetotolerans*, *Lactobacillus plantarum*, *Lactobacillus reuteri*, *Lactobacillus fermentum*, *Acetobacter pasteurianus* as reported by Ye, et al. [22]. Additionally, bacteriocins produced by LAB inhibit the growth of spoilage and pathogenic microorganisms [6]. Their metabolic adaptability allows LAB to survive and function in harsh conditions by altering cell membrane composition and employing proton pumps to maintain intracellular pH balance [23]. Furthermore, LAB such as L. *fermentum* are known to inhibit the formation of harmful advanced glycation end-products (AGEs), enhancing both the safety and sensory appeal of the final product [38]. Overall, the diversity and functional applications of LAB in vinegar fermentation underscore their indispensable role in producing high-quality vinegar with desirable sensory and microbial properties.

3. Vinegar Functional Compounds

Kinds of vinegar contain bioactive compounds such as organic acids, polyphenols, melanoidins, and tetramethylpyrazine. These compounds have been shown to offer a range of health advantages, including antibacterial and antioxidant properties. Regular vinegar consumption may contribute to weight management, improved blood pressure and glucose control, and better vascular health [10,13,39].

3.1. Organic Acids

Vinegar's acidity stems from a combination of organic acids. These acids can be categorized into volatile ones, such as acetic, formic, propionic, butyric, and quinic acids, and nonvolatile ones, including lactic, malic, pyroglutamic, citric, and succinic acids [13,40,41]. The origins of these organic acids can be traced back to both the fermentation process and the raw materials used. Acetic acid, predominantly formed during acetic acid fermentation, and lactic acid, a byproduct of alcohol fermentation, are the most abundant organic acids in vinegar [25,40,42,43]. Additionally, fruits contribute a range of organic acids, such as malic, citric, tartaric, lactic, succinic, and γ-aminobutyric (GABA) acids, to the overall composition of fruit vinegar [40,44,45]. The organic acids in the different types of vinegar are shown in **Table 1**. Among these, acetic acid reigns supreme, constituting a substantial portion (30-50%) of the total organic acid content in various vinegar types [46]. While acetic acid is the predominant volatile organic acid, lactic acid holds the title of the most abundant nonvolatile organic acid [45,47–49]. Other organic acids, such as formic, citric, malic, and succinic acids, have also been identified in vinegars, particularly balsamic vinegar, through advanced analytical techniques like nuclear magnetic resonance (NMR) [50]. Acetic acid, with its potent aroma and flavor, is a significant contributor to vinegar's sensory profile. However, the presence of lactic, tartaric, malic, and succinic acids acts as a counterbalance, resulting in a milder overall taste [46]. Beyond their organoleptic properties, organic acids in vinegar offer nutritional and functional benefits. Compounds like malic, citric, succinic, and lactic acids can be metabolized through the tricarboxylic acid cycle, a fundamental pathway for energy production from carbohydrates, lipids, and amino acids. Moreover, these acids, especially acetic acid, exhibit antimicrobial properties. Acetic acid, in particular, has demonstrated potent efficacy against harmful bacteria such as *Escherichia coli*

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O157:H7 [39]. Its antibacterial action is further enhanced when combined with citric acid. In addition to antimicrobial effects, acetic acid has garnered attention for its potential health benefits. Animal studies have indicated that acetic acid can contribute to lipid management by reducing cholesterol and triglyceride levels through mechanisms involving liver lipogenesis inhibition and increased bile acid excretion [51]. Furthermore, it has been shown to influence body fat accumulation by upregulating genes associated with fatty acid oxidation in the liver. Shen, et al. [52] research provides compelling evidence for the potential therapeutic benefits of acetic acid and vinegar in inflammatory bowel disease (IBD), specifically colitis. Their study demonstrated that both acetic acid (0.3% w/v) and vinegar (5% v/v) were effective in alleviating the symptoms of colitis induced by dextran sulfate sodium (DSS) in mice.

Table 1. Organic acids in different types of vinegars.

Vinegars	Organic acids	References
Traditional balsamic vinegar	Citric, tartaric, gluconic, malic, succinic , lactic and acetic, formic , and tartaric acids	[53–55]
Alcohol vinegar	Acetic acid	[56]
Cider vinegar	Acetic, citric, formic, lactic, malic, and succinic acids	[57]
Wine vinegar	Tartaric, malic, lactic, acetic, citric, succinic and formic acids	[47,57]
Tomato vinegar	Acetic, citric, formic, lactic, malic, and succinic acids	[57,58]
Plum vinegar	Acetic, tartaric, and lactic acids	[59]
Balsamic vinegar	Acetic, formic, citric, lactic, malic and succinic, tartaric, propanoic acid, 2 methylpropanoic acid, butanoic acid, 3-methylbutanoic acid, (E)- but-2-enoic acid, hexanoic acid, octanoic acid, 4-oxopentanoic acid, furan-2-carboxylic acid and 2-phenylacetic acids	[50,54,60]
Persimmon vinegar	Acetic, lactic, quinic, tartaric, propanedioic , malic, and succinic acids	[48]
Malt vinegar	Acetic, citric, lactic, and succinic acids	[56]
Apple vinegar	Acetic, lactic, quinic, tartaric, propanedioic, malic, succinic and citric acids	[48]
Kiwifruit vinegar	Acetic, lactic, quinic, tartaric, propanedioic, malic, succinic and citric acids	[48]
Sherry vinegar	Acetic, tartaric, lactic, malic, and citric acids	[61]
Zhenjiang vinegar	Acetic, 2-methyl propionate, 3-methylbutanoic, caproic, octanoic and propionic acids	[46]
Shanxi aged vinegar	Acetic, propionic, butyric acid, 3-methyl butyric, pentanoic, hexanoic, lactic, succinic, tartaric and citric acids	[49]
Black wolfberry vinegar	Lactic, acetic, sorbic, ascorbic, succinic, oxalic, malic, citric, tartaric and γ-aminobutyric (GABA) acids	[45]

3.2. Phenolic Compounds

The phenolic compounds that enrich vinegars primarily originate from the raw materials used in their production. Research has consistently identified a variety of phenolic acids within grain-based vinegars, including those derived from sorghum, bran, barley, pea, and rice bran. These phenolic acids encompass a diverse range of compounds such as gallic, ferulic, syringic, vanillic, protocatechuic, caffeic, chlorogenic, p-coumaric, p-hydroxybenzoic, sinapic, and salicylic acids [49,62,63]. Fruit vinegars, derived from fruits such as apples, grapes, pomegranates, blueberries, and black wolfberry, are abundant sources of phenolic acids. These compounds include catechin, syringic acid, gallic acid, chlorogenic acid, epicatechin, caffeic acid, ferulic acid, rutin, protocatechuic acid, and p-coumaric acid [45,64–66].

Phenolic acids are renowned for their antioxidant properties. They effectively neutralize harmful free radicals like hydroxyl radicals and superoxide anions through electron transfer, thereby preventing chain reactions. Additionally, these compounds can chelate with metal ions, inhibiting oxidation processes [67]. A detailed overview of the phenolic acid profiles in different vinegar types can be found in Table 2. A comparative analysis of phenolic compounds in various vinegars revealed significant disparities in their composition. For instance, Zhenjiang aromatic vinegar exhibited the highest concentration of gallic acid (555.3 ± 2.32 mg/L), while red wine vinegar was characterized by the most abundant caftaric acid (176.61 ± 0.24 mg/L) [48,68]. These findings underscore the notion that the specific phenolic profile of vinegar is contingent upon both the raw materials used and the

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manufacturing processes involved. A study by Budak, et al. [69] revealed that traditionally produced grape wine vinegar contains higher levels of chlorogenic and syringic acids compared to its industrially produced counterpart. Conversely, industrial grape wine vinegar exhibited a greater concentration of catechin. Regarding antioxidant capacity, as measured by Oxygen Radical Absorbance Capacity (ORAC) and Trolox Equivalent Antioxidant Capacity (TEAC) values, traditional grape wine vinegar outperformed the industrial variety. Additionally, both types of grape wine vinegar demonstrated superior antioxidant properties when compared to apple cider vinegar [69–71]. Furthermore, studies by Bertelli, et al. [72] and Xie, et al. [73] have indicated a positive correlation between aging time and the overall polyphenol content in vinegars. This suggests that the aging process significantly influences the phenolic composition of vinegar products. Research consistently demonstrates the potent antioxidant properties of vinegar phenolic compounds, contributing to reduced oxidative stress, improved lipid metabolism, blood pressure regulation, cardiovascular health, liver protection, and anti-aging effects. A strong correlation exists between phenolic content and antioxidant capacity in vinegars [40,73,74]. Comparative studies have shown that traditional vinegar production methods yield products with higher antioxidant activity than those produced industrially [65,75]. Analysis of traditional balsamic vinegars revealed that both melanoidins and polyphenols significantly contribute to their antioxidant properties [76–78]. Vinegar studies commonly identify gallic, caffeic, and catechin acids as prevalent phenolic compounds. However, flavonoid content in vinegars remains relatively lower. A notable exception is pomegranate vinegar, which Kharchoufi, et al. [79] found to contain 17 phenolic compounds—a significantly higher number than in other vinegars—as determined by UPLC-MS analysis. Protocatechuic acid was the most abundant phenolic compound in pomegranate vinegar, followed by gallic acid.

Cell and animal studies have shown that polyphenols in both grain and fruit vinegars possess potent antioxidant properties [72,80,81]. These compounds can effectively reduce oxidative stress and protect hepatocytes from damage by activating the Nrf2 signaling pathway [73,82]. Furthermore, vinegar polyphenols have been shown to lower blood lipid levels, regulate blood glucose, prevent blood clots, and exhibit anti-tumor effects [69,74,83,84]. These findings collectively highlight the significant health benefits of vinegar consumption, including improved cardiovascular health, liver protection, and overall well-being.

Table 2. Phenolic compounds in various types of vinegars.

Vinegar types	Phenolic compounds	References
Traditional balsamic vinegar	Furan-2-carboxylic, 5 hydroxyfuran-2-carboxylic,4-hydroxybenzoic, vanillic, protocatecuic, syringic, isoferulic, pcoumaric, gallic, ferulic and caffeic acids	[85]
Balsamic vinegar	Protocatechuic, gallic, p-coumaric, syringic, caffeic, ferulic, vanillic, salicylic, homovanillic, hydroxytyrosol, gentisic, p-carboxyphenol, protocatechuic, sinapinic and p-hydroxybenzoic acids and phenol, catechin, aesculetin, epicatechin, vanillin, coniferyl alcohol, 4-methylcatechol, syringaldehyde, isopropiovanillone, scopoletin, aceto-/isoacetovanillone, isopropiosiringone, acetosyringone, isoacetosiringone, syringol, coniferylaldehyde, sinapinaldehyde, tryptophol, o-vanillina, methyl vanillate, (m + p)-cresol, 4-ethylcatechol, ocresol, vanillyl ethyl ether, guaiacol, 4-methylsyringol, 4-vinylphenol, ethyl vanillate, 3,4-xylenol, 4-vinylguaiacol, ellagic acid, 4-ethylphenol, 4-methylguaiacol, 4-ethylguaiacol, 4-allylsyringol, eugenol and isoeugenol	[85,86]
Grape vinegar	Gallic, chlorogenic, caffeic, syringic, and ferulic acids and catechin and epicatechin	[65]

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Sherry vinegar	Gallic acid, Ellagic acid, protocatechuic, caffeoylquinic acid, protocatechualdehyde, tyrosol, p-OH-benzoic acid, catechin, p-OH-benzaldehyde, siringic, vanillin, caftaric, cis-p-coutaric, trans-p-coutaric, fertaric, caffeic, cis-p-coumaric, trans-p-coumaric, ferulic acids and quercetin 3-o-galactoside, quercetin 3-oglucuronide, kaempferol 3-o-galactoside, pelargonidine 3-o-galactoside, pelargonidine 3- o-robinobioside and aromadendrin 7-o-glucoside	[87,88]
Apple vinegar	Gallic, vanillic, chlorogenic, caffeic, p-coumaric, trans-ferulic, 4-pcoumaroylquinic, pcoumaroylquinic, p hydroxybenzoic, and protocatechuic acids, and (−)-epicatechin gallate and phloridzin	[48,89]
Apple cider vinegar	Gallic acid, catechin, epicatechin, chlorogenic acid, caffeic acid, and p-coumaric acid	[69]
Persimmon vinegar	Gallic, chlorogenic, caffeic, p-coumaric, trans-ferulic, Hydroxycinnamic, acids, (−)-epicatechin gallate, gallocatechin gallate, procyanidin A2, rutin epigallocatechin phloridzin, catechin hydrate, flavanols	[48,82]
Red wine vinegar	Gallic acid, protocatechuic acid, caffeic acid, vanillic acid, catechin, epicatechin, caftaric acid, syringic acid, ellagic acid, p-coumaric acid, ferulic acid and chlorogenic acid	[65,68]
Shanxi aged vinegar	Protocatechuic, p-hydroxybenzoic, salicylic, dihydrosinapic, p-coumaric, sinapic, dihydroferulic and ferulic acids	[90]
Pomegranate vinegar	Gallic acid, punicalagin, catechin, vanillic acid, syringic acid, galloylglucoside, protocatechuic acid, ethyl gallate, ellagic acid, chlorogenic acid, caffeic acid, p-coumaric acid, ferulic acid, ferulic acid hexoside, tyrosol and trans-p-Coumaric derivates	[79]
Zhenjiang aromatic vinegar	Gallic, vanillic, chlorogenic, p-coumaric and trans-ferulic acids, epicatechin and catechin hydrate	[48]

3.3. Melanoidins and Tetramethylpyrazine

Melanoidins, complex brown molecules formed during the Maillard reaction between sugars and proteins [91,92], are abundant in vinegars due to thermal processing and aging. Thermal treatment in grain vinegar production breaks down complex compounds into simpler sugars and amino acids, which then react to create melanoidins [93]. Aging concentrates these compounds and incorporates phenolic compounds from wood in fruit vinegar [87,94]. These high molecular weight melanoidin (10-100 kD) [95] are potent antioxidants, effectively binding metals [96] and gaining additional antioxidant power from incorporated phenolic acids [97]. Beyond their impact on flavor [91], melanoidin's in vinegar like Zhenjiang aromatic and traditional balsamic exhibit strong antioxidant properties [98]. These compounds significantly contribute to the vinegar's overall antioxidant capacity, as measured by 2,2′-azino-bis (3-ethylbenzothiazoline-6-sulfonic (ABTS) and ferric reducing antioxidant power (FRAP) assays [98], and protect the liver from oxidative damage [99]. Additionally, melanoidin's demonstrate antibacterial activity against common pathogens [100].

Tetramethylpyrazine (TMP), a compound produced through Maillard reactions and microbial fermentation, is a key component influencing the characteristics of vinegar. Its concentration fluctuates throughout the vinegar production process. For instance, TMP levels in Shanxi-aged vinegar increase during acetic acid fermentation after a low initial concentration [101]. In tartary buckwheat vinegar, TMP content rises initially but declines after three days of thermal processing [102]. Conversely, TMP accumulates over time in Zhenjiang aromatic vinegar [43]. A broader study of 137 vinegars revealed higher TMP levels in solid-state fermented vinegars than liquid-fermented ones [82,103,104], suggesting that thermal and aging processes are crucial for TMP formation. Beyond its impact on flavor, TMP offers potential health benefits. It has been linked to inhibiting platelet

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aggregation, vasodilation, lipid reduction, and antioxidant activity [105,106]. Studies on HepG2 cells have shown TMP's ability to improve lipid profiles by activating the PPARγ-LXRa-ABCA1 pathway, suggesting its potential in treating cardiovascular diseases [105].

3.4. Other Bioactive Compounds

Vinegar's diverse applications stem from unique production methods and specialized raw materials. For instance, Monascus aged vinegar contains lovastatin, a byproduct of microbial fermentation, which has been linked to reduced blood lipid and pressure levels [107]. Baoning vinegar, a renowned Chinese product, undergoes a meticulous process involving Daqu preparation, fermentation, boiling, and filtration. The addition of medicinal herbs like *Amomum villosum, Elettaria cardamomum, Eucommia ulmoides*, and *Angelica sinensis* to Daqu endows the vinegar with therapeutic properties, including spleen fortification, stomach nourishment, and overall health enhancement.

Intriguingly, Cao, et al. [108] discovered fluorescent nanoparticles (FNs) in mature Chinese vinegar. These approximately 1.40 ± 0.40 nm spherical particles are hypothesized to originate from the breakdown and restructuring of polysaccharides and proteins during the vinegar-making process. The interaction of these FNs with dopamine suggests potential health implications, warranting further investigation into vinegar's multifaceted benefits.

4. Functional Quality and Safety Improvements of Vinegar

The functional qualities and safety of vinegars will have impact on consumers' health. The bioactive components present in vinegar such as organic acids, melanoidins, polyphenols, and tetramethylpyrazine, can impact the functions of antioxidative activity, protect the liver, control blood pressure and glucose, regulate lipid metabolism, play anti-fatigue and anti-tumor, promotes digestion, stimulates the appetite, has antidiabetic effects, and show antimicrobial properties [40,109]. Bouazza, et al. [110] investigated lipid metabolism and liver damage in orally dosed high-fat fed rats with fruit vinegars made from pomegranate [*Punica granatum* L. (Punicaceae)], prickly pear [*Opuntia ficus-indica (L.)* Mill. (Cactaceae)], and apple [*Malus domestica* Borkh. (Rosaceae)]. They reported that these fruit vinegars regulate lipid metabolism and decrease liver damage in high-fat-fed rats.

Vinegar produced by spontaneous fermentation is vulnerable to consistent quality and complexity of microbiota. Therefore, the fermentation process should be monitored, controlled, and optimized to enhance the safety, flavor, and health benefits of the final vinegar. To avoid these challenges modern biological technology and vinegar fermentation have put the following strategies [111]: 1) Apply statistical techniques (partial least squares regression, two-way partial least squares regression, etc.) and metagenomics techniques to identify the metabolic functions of the fermenting microbiota. 2) Isolating strains having high-temperature tolerance, acid tolerance, and tolerance under pressure conditions using modern biological technology. 3) Regulate the key driving forces of the fermentation process using metatranscriptomic, metaproteomic, and metabolomics analysis methods. 4) Utilize bottom-up approaches, including classical microbiology and single-cell technology, along with top-down metagenomics, to enhance the qualitative and quantitative analysis of microbiota throughout the fermentation process. This approach enables precise microbiota modeling, contributing to the standardization and modernization of vinegar production. Generally, the methods employed to produce vinegar are classified as the slow method (Orleans method) and the rapid methods (submerged and generator methods) [109]. Many traditional vinegar production passes through five common processes: steaming the raw material, two-stage fermentation, fumigation, vinegar pouring, and aging. Figure 1 shows the sources of materials, fermentation methods, and other common processes during vinegar production.

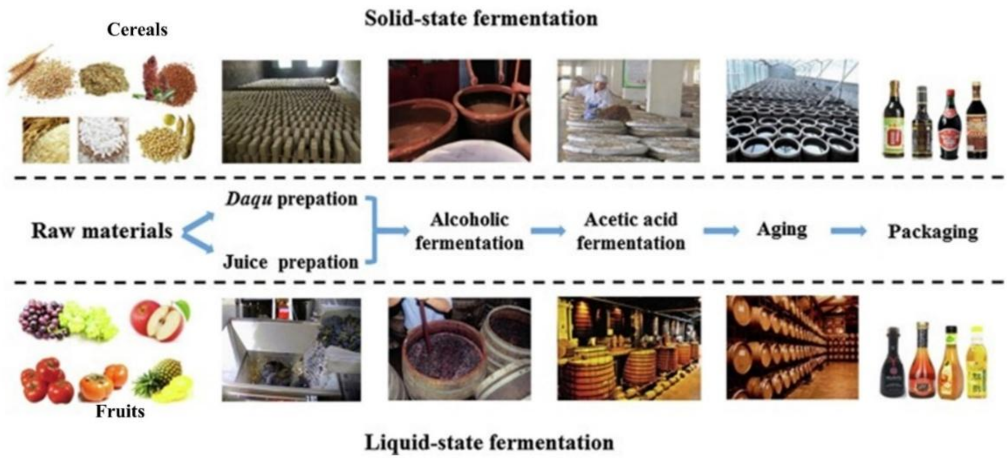

Figure 1. Raw materials and fermentation methods of vinegar production. (Reproduced from Xia, et al. [40] with permission from Journal of Functional Foods, copyright 2020).

4.1. Vinegar Quality Improvement

Quality of vinegars is dependent on finding appropriate additives, selecting perfect raw materials, mechanism of controlling environmental factors, and mechanisms of microbial biotransformation [111].

Molds, yeasts, and bacteria degrade proteins, carbohydrates and fats present in the fermentation substrate affecting the final vinegar quality by secreting enzymes such as amylase, glucoamylase, lipase, and proteases during the fermen-tation [111].

In the present world, special vinegars are produced by employing different acetification methods and the addition of extracts. In particular, Bertan, et al. [112] produced specialty vinegars from pineapple processing residues by enriching with phenolic contents and antioxidant potential from red-Jambo *Syzygium malaccense* leaf extract. The enriched specialty vinegars were found to contain polyphenols (443.6–337.3 mg GAE/L). Moreover, the acetification method applied reduced the saturation index and able to intensify the color of the final vinegar.

The maturation of young vinegar for an extended time helps to improve its flavor. The following latest advanced vinegar flavor maturation regulation technologies are currently developed [113]: 1) Microbial fortification or multi starter fermentation, in which the fermentation byproducts like total acids, esters, and aroma precursors facilitate vinegar flavor maturation. 2) Optimization of key production processes such as oxygen flow, fermentation temperature, and adjusting raw materials compositions enhance its flavor by generating alcohols, organic acids, polyphenols, and esters. 3) Applying novel physical processing like ultrasonication, ultra-high pressure, and microwave treatment promotes the conversion of alcohols into acids and esters in vinegar, which reduce flavor maturation time for over six months. For instance, Wang, et al. [46] investigated the application of slim-ultrasonic treatment to accelerate Zhenjiang vinegar maturation. They reported that many mature vinegar quality indicators such as reducing total amino acid from 1082.259 mg/100mL to 871.045 mg/100mL, enhancing volatile components (total esters, aldehydes and heterocyclic), and increasing total non-volatile organic acids from 202.59 mg/10mL to 233.87 mg/10mL were achieved at optimum ultrasonic power of 50 W/100mL, time of 75 min and addition of 0.75% (V/V) ethanol for aging vinegar.

Nutrients present in raw materials are converted into unique flavor-creating components (volatile or nonvolatile) of vinegar such as alcohols, aldehydes, phenols, organic acids, reducing sugars, and amino acids (Figure 2A). Hence, flavor quality and sensory perception of vinegars are directly affected by microbial composition and quantity [113]. Moreover, understanding the specific microbial genes, proteins, enzyme systems, and pathways during the vinegar fermentation helps to select and modify the excellent prominent microorganisms, which positively affect the final quality of vinegar. For instance, lengthy startup times can be reduced by controlling the ethanol oxida-tion

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pathway enzyme and cofactor Pyrroloqui-noline quinine (PQQ) of *Acetobacter*, and alleviating conflict among the increase of acetic acid production and cell fitness reduction [111]. Figure 2B depicts environmental factors that affect the reaction mechanisms of the main microorganisms during vinegar fermentation. The types of vinegars and methods employed for quality production are summarized in Table 3.

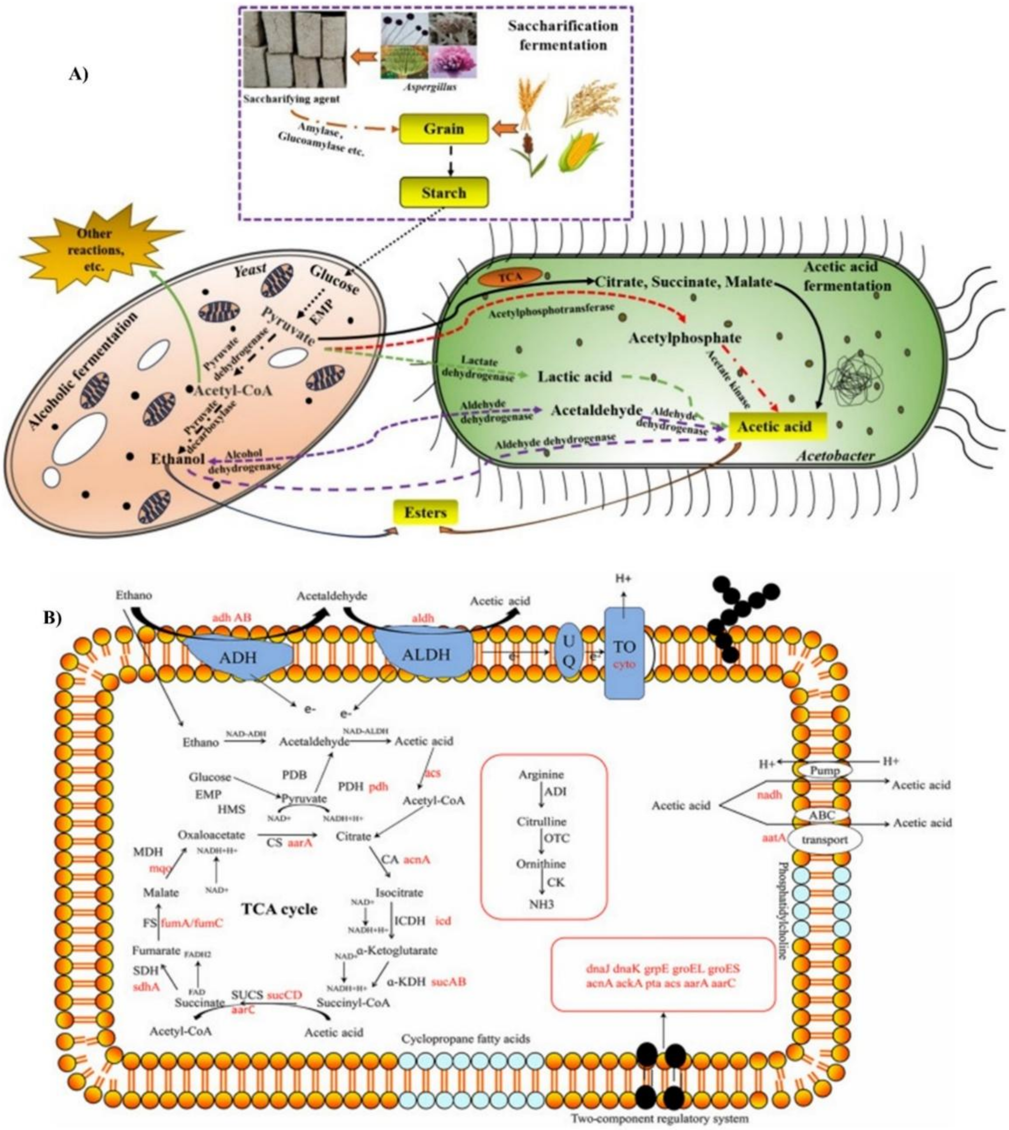

Figure 2. Vinegar fermentation mechanisms help to monitor the final vinegar quality. (A) Fermentation mechanism for the production of traditional Chinese vinegar (Reproduced from Zhang, et al. [113] with permission from Food Chemistry, copyright 2024). (B) Environmental factors that affect reaction mechanisms of core microorganisms and vinegar quality during the vinegar fermentation (Reproduced from Shi, et al. [111] with permission from LWT, copyright 2022).

Table 3. Types of vinegar and quality production methods.

Types of vinegars	Bacterial strain used for fermentation	Methods employed	Quality improvement applied	References
Black vinegar	*Acetobacter pasteurianus*	Saccharification of rice by *Aspergillus oryzae*	A year of aging	[114]

Cereal vinegar	*Acetobacter* sp.	Submerged fermentation of rice wine (Oryza sativa L.		[115]
Balsamic vinegar	*Gluconacetobacter europaeus* and/or *Acetobacter malorum*	Spontaneous acetification cooked of grape must using seed-vinager	Aged in wood barrels	[116]
White and red wine vinegar	*Gluconacetobacter europaeus* and/or *Acetobacter malorum*	Surface culture or submerged culture acetification	Aged in wood barrels (oak, chestnut, acacia and cherry)	[117]
Mature vinegar (Zhenjiang vinegar maturation)	*Acetobacter, Lactobacillus, Gluconoacetate, Bacillus*	Surface culture or submerged culture acetification	Aging by ultrasonic treatment	[46,118]
Aromatic vinegar (Zhenjiang aromatic vinegar)	*Lactobacillus acetotolerans, Lactobacillus plantarum, Lactobacillus reuteri, Lactobacillus fermentum, Acetobacter pasteurianus*	Solid-state fermentation	Addition of ground herbs	[22]
Fruit vinegar	Wild acetic bacteria strains	Acetification of pineapple pulp and peel wines using wild acetic bacteria strains	Leaf extract of Red-Jambo, *Syzygium malaccense*	[112]

4.2. Vinegar Safety Performance Improvement

Vinegars have side effects alongside to its beneficial health effects. The amount of consumption, concentration, duration, age, pregnancy case, etc. are determining factors for selecting consumers. In particular, health side effects like bowel movements and increased frequency of burping or flatulence were reported on apple vinegar. This effect was observed with the consumption of larger doses of apple cider (> 4 tablespoons daily) [119]. Undiluted or consumption of more than 2 tablespoons daily might cause episodes of hypoglycemia on patients having insulin-dependent diabetes [120]. However, other studies conducted on animals reported that there is no any adverse effects caused by the consumption of 14 mL apple vinegar/kg body weight daily for 18 weeks (equivalent to 1120 mL apple vinegar daily for a person having 80 kg weight) [121]. Hlebowicz, et al. [122] studied the effect of apple cider vinegar on delayed gastric emptying rats on diabetes mellitus patients. They reported that patients with insulin-dependent diabetes mellitus having diabetic gastroparesis are significantly affected by delaying gastric emptying rat, which have problems with glycaemic control.

Many quality and safety issues of vinegars could be produced by undesirable microorganisms during fermentation and/or aging/maturation. Vinegar quality and safety triggered by microbial contaminations (caused by *Bacillus* sp., *Acetobacter* sp., and *Lactobacillus* sp.) such as swollen vinegar, stickiness, gas-producing ones (*Acetobacter* sp. and *Bacillus* sp. and *Lactobacillus* sp.), and turbidity [123]. These vinegar spoilages caused by Lactobacillaceae (lower the vinegar total sugar and furfural) and a gas-producing bacterium named as *Acetilactobacillus jinshanensis* subsp. *aerogenes* can be available throughout the vinegar fermentation process. Although the *Acetilactobacillus jinshanensis* subsp. *aerogenes* are acid resistant, complete deactivation through heating (60 °C) is effective.

Safety of vinegar can be improved through technological-based microbial strain selection, proper maturation/aging and subsequently aging by adding oak chips. In particular, Lalou, et al. [124] produced persimmon balsamic vinegar through the pretreatment of oak chips which accelerated the aging conditions.

Enrichment of health-boosting and safety of vinegar bioactive components employing ultrasound treatment was achieved [125]. In this study, ultrasound treatment was applied for the enrichment of bioactive components of tomato vinegar and showed positive health effects. Moreover, Yıkmış, et al. [126] investigated ultrasound treatment of verjuice vinegar commonly produced from unripe grapefruit juice. The Verjuice vinegar produced by ultrasound treatment enriched its bioactive components which showed anticarcinogenic effects.

5. Vinegar Health Benefits

The principal functional goods of vinegars included antimicrobial, antioxidant, blood glucose and lipid metabolism control, weight loss, anti-inflammatory and anticancer potential.

5.1. Anti-Microbial Activity

Yagnik, et al. [127] investigated the impact of apple vinegar (ACV) on the growth of 2 resistant bacterial strains MRSA: methicillin-resistant *S. aureus* and *E. coli* resistant to cefepime-enmetazobactam and cefepime). The proteome approach of MRSA and E. coli displayed the inactivation of key metabolic enzymes for respiratory proteins and the replication of DNA. ACV perforated microbial cell membranes and organelles and therefore could alter vital proteins expression. This fact led to a reduction in the expression of proteins and only identifies ribosomal subunits proteins in *rE. coli*. In MRSA, extension factor phosphoglycerate kinase OS and iNOS present the sole existing proteins. Jia, et al. [128] demonstrated that *Eucommia ulmoides* leaves vinegar applied its antibacterial impact by a destructive bacterial cell wall and cell membrane, raising the cell permeability which led to the structural lesions and release of cell mechanisms, thus causing cell death.

Grain vinegars can efficiently inhibit respiratory pathogens viz. *M. catarrhalis*, *S. albus*, *D. pneumonia*, and *A. streptococcus*, however, apple vinegar powerfully inhibits the growth of pathogenic bacteria like *S*. epidermidis, P. aeruginosa, *P. mirabilis*, and *K. pneumoniae*. Al-Rousan, et al. [39] displayed that vinegar at 0.4% can decrease the *S. Typhimurium* and *E. coli* O157:H7 development and could prevent the *Yersinia enterocolitica* from growing at 0.156% (*v/v*) [39], On the other hand, some studies demonstrated that several the polyphenols presented in vinegar are liable for its developed antibacterial effect. Reygaert and Jusufi [129] reported that epicatechin-3-gallate may prevent microbial species at 720µg/mL. In addition, the epigallocatechin-3-gallate can inhibit of *S. aureus*, *S. mutans*, *E. coli* O157:H7, and *P. aeruginosa* 0.1, 0.1, 0.5, and 0.5 µg/mL [130].

The vinegar antifungal potential was documented. For instance, Yagnik, et al. [131] reported **a** MIC for ACV equal to 250 µg/mL against *C. albicans*. On another study, wood vinegar derived from cocoa pod shells present ϕ inhibitory zones covering till 12 mm against *C. albicans*, and 14 mm against *A. niger* which corresponds to 10% [132], while in the investigation of Oramahi and Yoshimura [133]**,** the 1% wood *Vitex pubescens vahl* vinegar was capable to prevent *Fomitopsis palustris*. *Chien*, et al. *[134]* pointed out that wood bamboo vinegar might stop the *Trichoderma viride* development. According to Shiah, et al. [135], organic acids and phenolics intervene with fungal wall cells, consequently augmenting the permeability.

5.2. Antioxidant Potential

Apropos antioxidant activity (Antiox. Act) outcomes of diverse fruit vinegars, Kelebek, et al. [70] stated that the grape vinegars Antiox. Act, expressed by DPPH, extended from 5 to 14 mM Trolox/L and from 7-18 mM Trolox/L (ABTS)). Regarding apple vinegars, this activity corresponds to 2-15 mM Trolox/L (DPPH) and 4-20 mM Trolox/L (ABTS). In the studies conducted by Xia, et al. [136], the

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antioxidant potential of traditional balsamic vinegar was improved with ripening time. By comparing industrial processes, it appeared that traditional vinegar showed the highest Antiox. Act compared to manufacturing ones [75]. On the other hand, many investigations evidenced that vinegar phenolic substances possess an elevated connection with the antioxidant potential [73,74]. According to Tagliazucchi, et al. [98], it has been validated that the Antiox. Act of traditional balsamic vinegar was principally linked to the melanoidins and polyphenolic fractions. Xia, et al. [40] stated that the polysaccharides fraction of buckwheat vinegar essentially comprised the Ara, Xyl, Glu, Man, and Gal presented a good antioxidant power. By examining the in vitro digestion impact of the digestion on the jujube vinegar antioxidant activity, Li, et al. [38] confirmed that while gastric digestion decreased the content of total polyphenolics (TPC) at 55%, gastric acid and gastric protease could preserve a high antioxidant level (DPPH). In this study, the intestinal digestion, the TPC augmented ~ 9 %, and the DPPH· was also enhanced to 24% in the first 30 min. Besides, cell culture and animal investigations established that polyphenols in fruit and grain vinegars may decrease the free radical damage [137,138] and protect the hepatocytes versus free radical damage through the nuclear factor erythroid-2-related factor 2 (Nrf2) signal route [73].

5.3. Anti-Inflammatory Activity

Several investigations have exposed that fruit vinegar could govern the proinflammatory cytokines product [139,140], and it enhances intestinal permeability and governs the microbiota, thus hindering the access of damaging elements of the bloodstream and monitoring the inflammation progression Meng, et al. [141]. Furthermore, it should be noted that fruit vinegar consumption frequently decreases the inflammatory cytokines, cyclooxygenase (COX)-2, nitric oxide (NO), inducible nitric oxide synthase (iNOS), and mitogen-activated protein kinase (MAPKs) [142,143].

Throughout the vinegar aging progression, vinegar covers remarkable amounts of functional and living microorganisms and lipopolysaccharides [144]. By promoting the phagocytic impact and supporting the immune system, these molecules regulate macrophage function and control allergy, cancer, and inflammation [127]. As an illustration, nipa vinegar touches gut microbiota, expanding the population of *ProteobacteriaphylumVerrucomicrobia*, and diminishing the gut Firmicutes/Bacteroidetes rate [137]. Some studies have revealed that the organic acids present in vinegars control the gut community by governing the gastrointestinal pH and increasing pancreatic activity [145]. Furthermore, organic acids prevent the occupation and adherence of invasive and pathogenic microorganisms [146], and boost barrier function and intestinal morphology [147]. As a model, the investigation reported by Jiang et al. [148] announced that the vinegar enhanced the detachment of lamina propia of the intestinal mucosa, inflammatory cell permeation in the reduction of wall intestinal: p65 and ICAM-1 expression, and augmented E-cadherin in the rats' intestinal tract [148]. Additionally, the control of the intestinal microbiota recovers the course of short-chain fatty acids (SCFA) production concerned with the mechanism of the inflammatory pathways that engaged in several diseases [149].

Likewise, vinegar improves diverse diseases in which the inflammatory action arranges their development, including arthritis, atopic dermatitis, colitis, and oxidative stress [150]. Fruit vinegar was considered to govern the production of inflammatory markers, increase the immune reaction, and ensure the gut microbiota that plays an essential part in asthma pathophysiology [151]. During 24 days, the oak wood vinegar reduced the IgE production in 2,4-dinitrochlorobenzene (DNCB)-induced contact dermatitis mice model [152]. Moreover, nipa vinegar effectively showed its capability to overturn the inflammatory intermediaries' expression like iNOS and NF-kB, inducing the NO levels to decrease. In this line, NO at high levels circuitously triggers Th2 cells, which are concerned in asthma physiopathology [153].

To reduce the inflammatory cell permeation and arthritic index in rats [154], inspected the capacity of a pioneering preparation of the vinegar Pangolin Scale Processed (PSP). PSP dropped the serum levels of inflammatory cytokines, comprising TNF-α and IL-1ß [154].

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In the animal model, tetramethylpyrazine, an active compound of vinegar, had been associated in the inhibition of acute pancreatitis by hindering the nuclear factor-kappa B (NF-κß) [155]. Choi, et al. [142] noticed that vinegar amended pro-inflammatory markers *viz.* NO, iNOS, TNF-*α* IL-6, and MCP-1, which are convoluted in the inflammatory reaction. Furthermore, ligustrazine has displayed talented leads to acute pancreatitis, endorsing acinar cell apoptosis at the initial step and attenuating the Erk MAP and p38 pathways [156]. **Table 4** summarizes some examples of vinegar functions on health. Figure 3 represents the functional qualities and health benefits of vinegar for human consumption.

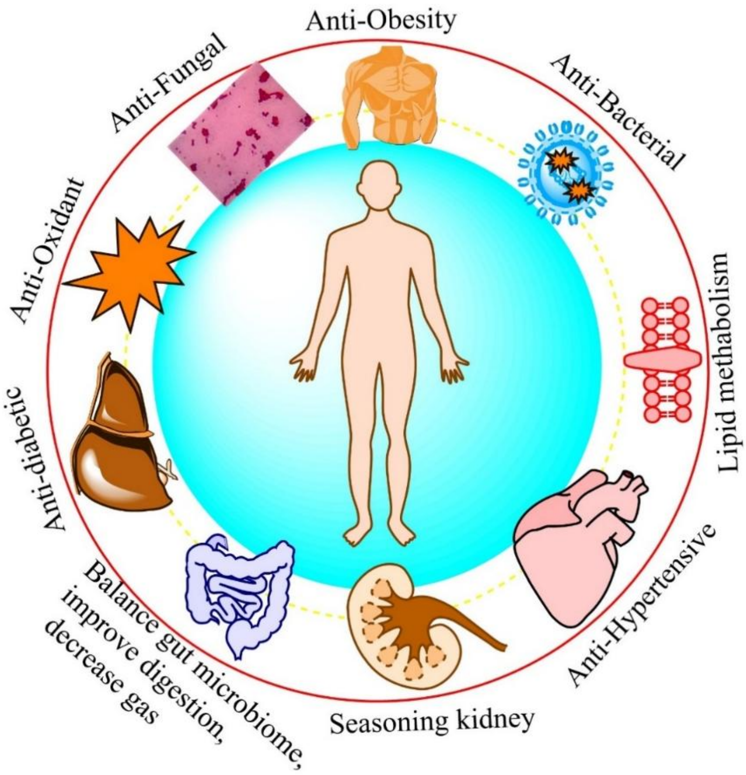

Figure 3. Functional qualities and health benefits of vinegar for human consumption.

Table 4. health benefits of vinegar.

Vegetable vinegars	Target activity	Objective of the study	Main findings	References
Leaves of Eucommia ulmoides	Antibacterial potential	Study the mechanism of action against B. subtilis	-↗antibacterial effect and yeast - Cell wall and cell membrane were damaged - ↗ increasing the cell permeability	[128]
Grape, apple, Artichoke, pomegranate, Apple-Lemon, Hawthorne and sour cherry	Antimicrobial potential and antiradical activity	Distinguish between the traditional and industrailised Turkish vinegars.	-↗ antimicrobial activity in traditional vinegars compared to industrial ones -↗ antiradical potential of pomegranate vinegars compared to industrial ones	[157]

Black vinegar	Antiox. Act and in vivo lipid-lowering	Investigate these activities via a hamster model	- ↘ weight gain -↗ lipid contents and hepatic Antiox. Act	[158]
Tomato	Lipid and Glu metabolic enzyme	-Mechanism investigation -Arbitrated the anti-insulin and anti-obesity effect	-↘ fat accumulation -Variations arbitrated by PPARa and AMPK increased expression.	[159]
Tomato	Anti-obesity impact	Assess the efficiency in lipid accumulation	-Inhibition of lipid formation.	[160]
Cereal	Hepatoprotective impact	Explore the hepatoprotective impact	Changes in gut microbiota	[161]
Cereal	Impact on the spontaneous colitis impact	Explore the process of spontaneous colitis and investigate the variations in the in the epithelial wall function, inflammation and gut microbiota.	-Improvement of epithelium damage, -Inhibition of myeloperoxidase activity and malondialdehyde (MDA)	[162]
Shanxi-aged vinegar	Anti-inflammatory activities	Investigate the anflammatory mechanism	-Enhancement of the lipid, inflammatory stress and oxidative stress.	[163]
Shanxi-aged vinegar	Impact on gut microbiome and metabolome	Investigate the immune/inflammation factors and explore the in vivo impact of vinegar on gut microbiome and metabolome.	- ↘Inflammatory factors - Vinegar consumption changed gut microbiota structure	[164]
Orange, mango, cherry and banana	Antioxidant potential	Investigate the kinetics, chemical profile and Antiox. Act	-Total antioxidant activity was assessed at 8 and 40 times greater than a commercial vinegar.	[165]
Orange	Antioxidant potential	Investigate the fluctuations of chemical profile and Antiox. Act during fermentation.	Antiox. Act was linked to ascorbic acid and phenolic compounds levels.	[166]
Rosehip fruit (Rosa canina L.)	Antioxidant potential	Expose the chemical profile and Antiox. Act	-↗ of antioxidant activity linked to the ↘ of flavonoids	[167]
black tea	Antioxidant potential	-Evaluation the chemical profile and Antiox. Act	- ↗of organic acids contents, volatile compounds and the antioxidant activity	[168]
Apple Cider	Antioxidant potential	Investigate the change of antioxidant properties and bioactive compounds	→Antioxidant activity and phenolic substances during the acetic acid fermentation.	[169]

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green jujube	Antioxidant potential	Study the impact of the in vitro gastrointestinal digestion on the Antiox. Act and hypolipidemic potential	-↗ correlation between Antiox. Act, TPC, TFC, and total acid contents -weak correlation with cholesterol adsorption capacity/antioxidant capacity	[38]
nipa palm	Antioxidant and anti-tyrosinase activities	-Characterize chemical profile, Antiox. Act, and anti-tyrosinase potential. -Perform molecular docking study and molecular dynamic simulation	-Concentration-dependent anti-tyrosinase activity and antioxidant potential	[170]
Wood	Antimicrobial and anti-inflammatory potential	-Asses the in vivo inflammatory activity of the mammalian macrophages and antimicrobial activity against pathogenic bacteria and fungi	-Stimulation of mammalian macrophages by lipopolysaccharide -High antimicrobial activity but no anti-bacteriophage activity	[171]
Cudrania tricuspidata Fruits (CTFV)	Anti-Inflammatory potential	In vitro anti-inflammatory impacts	CTFV reduced inflammatory reaction by improving inflammatory factors	[142]
vinegar-baked Radix Bupleuri (VBCP)	Anti-Inflammatory potential	-study the impact of extraction techniques on the physicochemical properties and biological activities of VBCP	ammonia-assisted extraction is an effective tool to achieve high anti-inflammatory	[172]
Apple	antioxidant, antimicrobial, antidepressant and anti-inflammatory activities	Study the biological activity of our different apple cultivars, as well as physicochemical attributes and chemical composition	-↗ antidepressant impact -effective against bacteria, -↗ antioxidant activity	[173]
Curcuma phaeocaulis	anti-angiogenic effect	Evaluation of anti-angiogenic impact and toxicity of C. phaeocaulis via zebrafish and rat models.	-↘ toxicity and ↗anti-angiogenic activity	[174]

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6. Conclusions

This review highlights vinegar's remarkable versatility and potential health benefits driven by its bioactive components, including organic acids, polyphenols, melanoidins, and tetramethylpyrazine. These compounds collectively contribute to vinegar's antimicrobial, antioxidant, and anti-inflammatory properties, as well as its potential roles in glucose regulation, lipid metabolism, and weight management. LABs, crucial to the fermentation process, contribute not only to vinegar's unique sensory qualities but also to its functional benefits. Additionally, LAB's presence enhances the probiotic potential of vinegar, while melanoidins and polyphenols contribute significantly to its antioxidant capacity.

Vinegar production methods, such as traditional aging and modern fermentation optimization, influence its bioactive profile and health benefits. Advances in fermentation technology, including microbial selection, controlled fermentation environments, and novel maturation techniques, are essential for ensuring quality and safety while enhancing vinegar's health-promoting properties. These improvements make vinegar a promising functional food ingredient with applications in diet and therapeutic fields.

Overall, this review underscores the diverse applications of vinegar and supports its inclusion in diets aimed at health improvement. Further research is encouraged to explore vinegar's therapeutic applications in clinical settings and its potential as a functional supplement in food and nutrition.

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