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MINI-REVIEW

Microbial diversity and their roles in the vinegar fermentation process

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Abstract Vinegar is one of the oldest acetic acid-diluted solution products in the world. It is produced from any fermentable sugary substrate by various fermentation methods. The final vinegar products possess unique functions, which are endowed with many kinds of compounds formed in the fermentation process. The quality of vinegar is determined by many factors, especially by the raw materials and microbial diversity involved in vinegar fermentation. Given that metabolic products from the fermenting strains are directly related to the quality of the final products of vinegar, the microbial diversity and features of the dominant strains involved in different fermentation stages should be analyzed to improve the strains and stabilize fermentation. Moreover, although numerous microbiological studies have been conducted to examine the process of vinegar fermentation, knowledge about microbial diversity and their roles involved in fermentation is still fragmentary and not systematic enough. Therefore, in this review, the dominant microorganism species involved in the stages of alcoholic fermentation and acetic acid fermentation of dissimilar vinegars were summarized. We also summarized various physicochemical properties and crucial compounds in disparate types of vinegar. Furthermore, the merits and drawbacks of vital fermentation methods were generalized. Finally, we described in detail the relationships among microbial diversity, raw materials, fermentation methods, physicochemical properties, compounds, functionality, and final quality of vinegar. The integration of this information can provide us a detailed map about the microbial diversity and function involved in vinegar fermentation.

Keywords Vinegar · Microbial diversity · Fermentation · Acetic acid · Starter culture

Introduction

Vinegar is one of the most widespread and common acetic acid-diluted solution products in the world (Solieri and Giudici 2009). It is available in every country in distinct varieties (Ubeda et al. 2011a, 2012), and it has been produced since ancient times from a double fermentation of any fermentable sugary substrate (Solieri and Giudici 2008). Vinegars are produced from many kinds of raw materials (e.g., cider, wine, and sorghum) by a variety of different fermentation methods, and their organoleptic and chemical properties are determined by many factors (Natera et al. 2003). According to the type of raw materials, researchers have classified vinegars into three categories: vegetable vinegars (rice vinegar, onion vinegar, and tomato vinegar), fruit vinegars (cider vinegar, mango vinegar, and pineapple vinegar), and animal vinegars (honey vinegar and whey vinegar) (Solieri and Giudici 2009). Vinegar plays an important role in the quality of people's life and culture, and it has a long history in the world (Mazza and Murooka 2009). The majority of vinegars, especially those from acidic and sugary fruits, are very easy to make, so the science and technology of vinegars developed relatively slowly through time. However, there is currently an urgent demand to improve the technology and increase scientific knowledge of vinegar production. Moreover, using starter cultures in vinegar production is the main technological improvement in innovations of vinegar production. To develop the starter cultures, we must determine which microorganisms

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can be used in vinegar production (Gullo and Giudici 2008). Although numerous microbiological studies have been conducted to examine the process of vinegar fermentation, microbial diversity and their functions involved in vinegar fermentation have not been summarized systematically. No study has thoroughly expounded the relationships among microbial variations, raw materials, fermentation methods, and other determinant factors in vinegar fermentation. Consequently, to obtain a comprehensive understanding of the science and technologies of vinegar production, more studies need to be conducted on microbial diversity, variations in vinegar fermentation, and their functions in vinegar production.

Different types of vinegars have various functions. Some can be used as preservatives or condiments, and some of them are also believed to be drinks (Solieri and Giudici 2009). Some kinds of vinegars are also used to treat diseases in traditional Chinese medicine. Many studies have also indicated that vinegar has a wide spectrum of physiological effects, such as alleviating exhaustion, preventing obesity, and regulating blood pressure and blood glucose (Fan et al. 2009; Gu et al. 2012; Kahramani et al. 2011; Kondo et al. 2001; Sugiyama et al. 2003). In addition, it can be used as a natural insecticide, antigermination agent, and termiticide. Vinegar contains a large amount of trace components, such as polyphenols and flavonoids, although its main ingredients are acetic acid and water. All of the compounds in vinegar contribute to its taste, smell, and specific functions (Zhang et al. 2006). Therefore, analyzing the discrepancy among the key compounds in different types of vinegar is important to understand the relationship between compounds and functionality of vinegar.

The manufacture of some vinegars usually includes three stages of fermentation (Solieri and Giudici 2009). The first stage is starch saccharification. The second step is alcoholic fermentation (AF), which is the conversion of fermentable sugars into ethanol mainly by yeast. The third stage is acetic acid fermentation (AAF), which is the oxidation of ethanol to acetic acid by acetic acid bacteria (AAB) (Adams 1997). However, not all vinegar production processes involve starch saccharification because the occurrence of AF either coincides with saccharification or appears after saccharification. For example, in fruit vinegar production, the occurrence of AF coincides with saccharification because no distinct saccharification step exists in fermentation. By contrast, some rice and cereal vinegars that are produced with starchy raw materials have a distinct saccharification step (Haruta et al. 2006; Lee et al. 2012). However, AF and AAF are distinctly different and have separate biochemical processes, and both are the results of the action of microorganisms. Considering that the production of all vinegars has AF and AAF stages, we defined vinegar fermentation as a double fermentation process (Casale et al. 2006). Vinegar fermentations were rarely inoculated with a pure culture until 1907 (Nanda et al. 2001), and the fermentations were always initiated by mixed strains that consisted of mold and yeast populations and succeeded and ultimately dominated by acid-tolerant species (Teoh et al. 2004). Furthermore, given that the metabolic products from the fermenting strains are directly related to the quality of the final vinegar, analyses of the microbial diversity and features of the dominant strains involved in different fermentation stages are desirable to improve the strains and stabilize fermentation (Fleet 1999; Gullo and Giudici 2008; Hidalgo et al. 2010; Wu et al. 2012a).

This review aimed to gain insight into the microbial diversity involved in vinegar fermentation and improve the biotechnological process of vinegar production by comparing and analyzing the diversity of microorganisms involved in both fermentation stages (AF and AAF). This review is expected to provide a better understanding of microbial diversity and the roles of microorganisms in vinegar production. This review will mainly point out the diversity of microorganisms associated with each fermentation stage and describe the discrepancy among the key compounds and physicochemical properties of different vinegars. Finally, this review analysis will focus on the reasons why different vinegars select disparate strains as starter cultures, why various species are involved in dissimilar fermentation processes, and why we should choose disparate fermentation methods in the production of different vinegars. This review will establish a better understanding of the relationship between microbial diversity and other determinant factors in establishing the quality of vinegar.

Manufacturing process of vinegar

Common procedure for vinegar production

The present production of vinegar has evolved from a simple artisanal scale to a large-scale industrial process. Meanwhile, the common procedure for vinegar production is graphically displayed in Fig. 1.

Ethanol production

Raw material preparation

The first stage of the brewing process is to prepare raw materials by milling (Grierson 2009; Li et al. 2015). The purpose of milling is to break the raw materials to release starch and sugar for increasing water absorption and obtaining a desirable cohesion of the mass (Zheng et al. 2011).

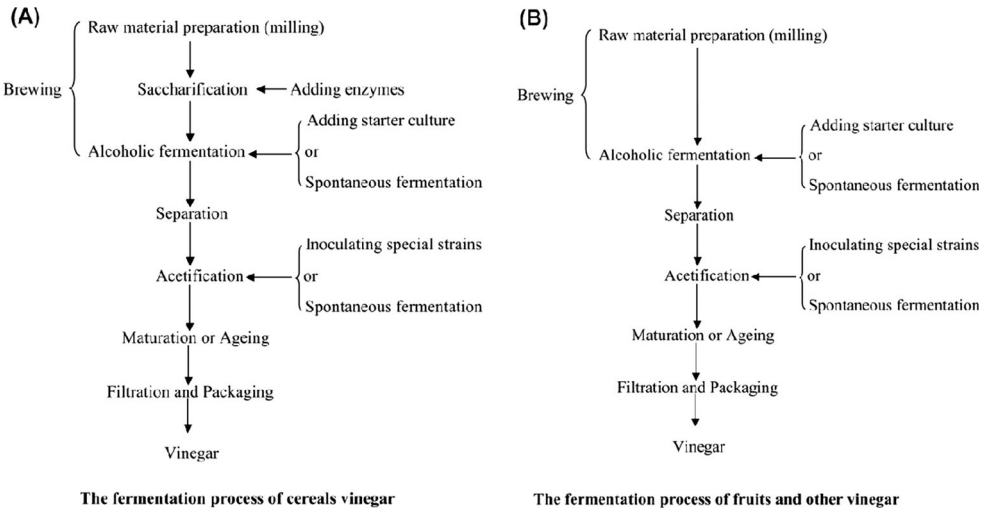

Fig. 1 **a**, **b** The production process of vinegar

Saccharification

The second stage in the brewing process is the conversion of starch to sugars to prepare for AF. In this stage, some enzymes (α-/β-amylase, protease, and β-glucanase) may be added to better convert the starch to fermentable sugars, and they play a crucial role in productivity and directly affect the flavor formation of traditional Chinese vinegar (Li et al. 2015). Only some rice and cereal vinegar fermentation processes require a distinct saccharification step to convert the raw materials to sugars, whereas no saccharification step exists in sugar-rich fruit vinegar production (Fig. 1). For instance, traditional balsamic vinegar (TBV) production has no saccharification stage, but it requires cooking to improve the concentration of fermentable sugar before AF, and cooking is generally stopped when the grape must concentration reaches 35–60° (°Brix) of soluble solids (Giudici et al. 2009).

Alcoholic fermentation

The last stage of the brewing process is the conversion of fermentable sugars to ethanol (Solieri and Giudici 2009). This stage is an anaerobic fermentation stage, and it needs to be kept in a controlled temperature of 20–30 °C (Grierson 2009; Wu et al. 2012a). AF of fruit vinegar is mainly carried out by *Saccharomyces cerevisiae*, and it can be performed either by natural spontaneous fermentation or pure culture inoculation. In simple artisanal production, AF always occurs spontaneously, but in large-scale industrial production, AF is performed by adding a starter culture mainly from the genus *Saccharomyces* (Adams 1997).

Separation

After the AF stage, the yeasts are inactive and begin to autolyse. The microbial cells will hinder the next fermentation stage, so removing these cells by high-speed centrifugal separation is imperative (Grierson 2009).

Acetous fermentation

Acetous fermentation is the aerobic oxidation of ethanol to acetic acid, which is a biotransformation process performed by AAB (Horiuchi et al. 2000a, b). This stage is a fairly slow open fermentation process, and it needs to provide a suitable habitat for the *Acetobacter* species, so the fermentation vessel is not covered by any lid in the AAF stage (Wu et al. 2012a). In cereals and traditional Chinese vinegar production, after AF, vinegar "seeds," which come from the last batch of vinegar Pei, are added into the acetator and mixed well with wheat bran and coarse rice hull, which are used to increase the loose interspace for heat discharge and oxygen uptake and to promote AAB growth and metabolic activities (Chen et al. 2009). In this step, the temperature in the urn should be stabilized at 38–46 °C by pressing and turning over the vinegar Pei to decrease the rate of ethanol consumption and reduce oxygen supply and heat production. Normally, vinegar Pei is turned over once a day, and this step generally lasts about 20 days (Xu et al. 2011a). In contrast, the AAF of fruit vinegar is different from cereal vinegar. For example, apple cider vinegar (ACV) after AF contains a high concentration of alcohol that needs adjusted to be 7–8 % *v/v* by adding water. It is then mixed with ACV from previous cider acidification and inoculated with AAB species to accomplish the AAF step (Joshi and Sharma 2009; Kocher et al. 2007). In the past, vinegar was derived from the spontaneous acidification of wine; thus, the acetification of traditional vinegar production is spontaneous fermentation, so no selected strains are inoculated in this process (Adams 1997; Wu et al. 2012a). However, to improve acetification rates, the "mother of vinegar" or a starter culture of beneficial strains is inoculated in the AAF stage (González and De Vuyst 2009; Gullo et al. 2009). Several studies proved

that a huge improvement in the ethanol oxidation rate is achieved by inoculating specific AAB (Kocher et al. 2007; Sievers et al. 1992). From a technological perspective, many different kinds of fermentation methods are applied in this stage for the purpose of improving vinegar manufacture technology (De Ory et al. 2004; Kaur et al. 2011; Solieri and Giudici 2009). The AAF of vinegar production can be achieved either by traditional slow methods, such as surface culture fermentation (Tesfaye et al. 2002b) or quick submerged methods, based on different kinds of acetators that increase acetic acid yield and acetification rate using semicontinuous or continuous processes (Joshi and Thakur 2000).

Maturation or aging

After acetification the "rough stock vinegar" will be stored in storage vessels and allowed to be saved for at least 3 months (Joshi and Sharma 2009). Furthermore, traditional wine vinegar (WV) production requires maturation in wood for many years to obtain a high acetic degree (Tesfaye et al. 2002b). At this stage, we can obtain a high concentration of acetic acid and a low concentration of alcohol, and important chemical changes occur during aging, such as the formation of furan derivatives and hydroxymethylfurfural, because of low pH and water activity (Solieri and Giudici 2008).

Microbial diversity involved in vinegar production

Microbial diversity involved in saccharification

Saccharification is actually the immediate hydrolysis of starch by microbial metabolisms and enzymes from Qu to produce saccharified mash, and this step is the start of AF (Chen et al. 2009). The significant saccharification stage is only presented in specific vinegar fermentation, in which raw materials as cultures contain high starch levels. The fermentation of fruit vinegars or other vinegars that use raw material as cultures with high sugar does not have this stage. Hence, to better illustrate ethanol production in all types of vinegar, we named saccharification as the initial stage of AF. Even though only a few molds are involved in the initial stage of AF, they play a pivotal role in the final quality of vinegar because they can produce a wide range of secondary metabolites, including flavor and odor components, pigments, and compounds with antibiotic properties. Moreover, the release of many kinds of enzymes is a common characteristic of most molds that has been largely exploited in industrial vinegar production (Rainieri and Zambonelli 2009). In the initial stage of AF, we require a variety of amylases and hydrolases to help the conversion of starch to fermentable sugars, so most molds may be artificially inoculated in early AF. *Aspergillus oryzae* has powerful ability to release amylase and proteolytic enzymes, which can rapidly convert starch into sugar (Hashimoto et al. 2013; Li et al. 2015). In addition, although the genera *Bacillus* are contaminants in most vinegar fermentation, some *Bacillus* species are considered to be functional microbes, responsible for the formation of a range of lytic enzymes, substrates for early AF, and flavor compounds (Zheng et al. 2011). For example, *Bacillus amyloliquefaciens* can produce amylases to degrade starch into maltose or dextrin and further to glucose (Li et al. 2014; Zheng et al. 2011). In rice vinegar and cereal vinegar, *As. oryzae* is the dominant mold species and *Bacillus* species are the functional bacteria involved in the initial stage of AF. Table 1 shows that the dominant species involved in the initial stages of AF are mainly from the genera *Aspergillus*, *Absidia*, *Mucor*, and *Rhizopus*. For example, in rice vinegar, the saccharification of rice is mainly by the Koji mold *As. oryzae* (Hashimoto et al. 2013; Nanda et al. 2001).

Microbial diversity involved in alcoholic fermentation

Vinegar is the product of double fermentation, which is carried out by different types of microorganisms acting in different fermentation stages (Fig. 2) (Rainieri and Zambonelli 2009). Tables 1 and 2 summarize the groups of microorganisms that have been isolated and reported from different types of vinegar. AF is the first important step to provide flavor into vinegar (Sudheer Kumar et al. 2009), and the most flavorful compounds are the metabolic products from fermentation strains. Meanwhile, different raw materials and fermentation conditions may cause significant differences in microorganisms between AF and AAF (Li et al. 2014). Thus, the microbial diversity in different fermentation stages should be analyzed.

As shown in Table 1, different kinds of strains are isolated in AF of different types of vinegar. AF of all vinegars mainly involves yeast species and only a few other genera. This phenomenon is due to the fact that conversion of fermentable sugars into ethanol is mainly performed by yeast. The metabolic activity from yeasts can remarkably increase the alcoholic degree at the end of AF, which also inhibits the growth and metabolism of most other microorganisms (Wu et al. 2012a). Generally, yeasts grow well at pH 3–5, and they sometimes grow with difficulty at neutral pH. They prefer acidic substrates and generally ferment sugars vigorously at concentrations of up to 20 %, but fermentative metabolism slows down at higher concentrations. When the sugar concentration is above 50 %, osmotic pressure will become excessively high, which can inhibit the growth and metabolism of most yeast species (Rainieri and Zambonelli 2009). However, several species that belong to the genus *Saccharomyces* multiply faster than other yeast species and dominate in terms of the percentage because the fermentation conditions are more suitable for their growth. Moreover, at high temperature and high sugar concentration, *S. cerevisiae* also exhibits strong

Table 1 Strains isolated in different types of vinegar's alcoholic fermentation

Vinegar	Abbreviation	Strains	References
Rice vinegar			
White rice vinegar	WRV	1. *S. cerevisiae*; 2. *Zygosaccharomyces* spp.; 3. *Candida* sp.; 4. *As. oryzae*	Haruta et al. (2006), Okazaki et al. (2010), Solieri and Giudici (2009)
Chinese rice vinegar	CRV	1. *S. cerevisiae*; 2. *Sp. fibuligera*; 3. *P. kudriavzevii*; 4. *As. oryzae*; *As. niger*; *As. candidus*; 5. *R. microspores*; 6. *Eu. herbariorum*	Chen and Xu (2010), Li et al. (2014)
Kurosu (Black rice vinegar)	BRV	1. *S. cerevisiae*; 2. *Pc. acidilactici*; 3. *La. lactis*; 4. *As. oryzae*; *As. awamori*; *As. usami*	Hashimoto et al. (2013), Murooka and Yamshita (2008), Solieri and Giudici (2009)
Komesu (Amber rice vinegar)	ARV	1. *S. cerevisiae*; 2. *As. oryzae*	Murooka and Yamshita (2008), Solieri and Giudici (2009)
Zhengjiang aromatic vinegar	ZAV	1. *S. cerevisiae*; *S. cariocanus*; *S. paradoxus*; *S. bayanus*; 2. *Se. complicate*	Xu et al. (2011a)
Cereal vinegar			
Sorghum vinegar	SV	1. *S. cerevisiae*; 2. *Ca. saccharolyticus*; 3. *Hansenula* spp.; 4. *As. oryzae*; 5. *Saccharum* spp.; 6. *C. krusei*	Dien et al. (2009), Hamad et al. (1992), Panagiotopoulos et al. (2010), Solieri and Giudici (2009), Tew et al. (2008)
Cereal/Grain vinegar	C/GV	1. *S. cerevisiae*; 2. *C. berkout*; 3. *Hs. anomala*; 4. *Lb. sakei*; *Lb. plantarum*; *Lb. fermentum*; *Lb. homohiochii*; *Lb. heterohiochii*; *Lb. fructivorans*; 5. *Mucor* spp.; 6. *Monascus* spp.; 7. *Rhizopus* spp.; 8. *Absidia* spp.; 9. *Le. mesenteroides*	Chen et al. (2009), Hammes et al. (2005), Wu et al. (2010)
Shangxi aged vinegar	SAV	1. *S. cerevisiae*; 2. *Lb. fermentation*; *Lb. plantarum*; *Lb. buchneri*; *Lb. casei*; 3. *Pc. Acidilactici*; *Pc. pentosaceus*; *Pc. anomala*; 4. *C. berkout*; 5. *G. oxydans*; 6. *Le. mesenteroides*; *Le. citreum*; 7. *W. confuse*; 8. *A. indonesiensis*; *A. orientalis*; *A. senegalensis*; *A. malorum*	Ehrmann et al. (2009), Solieri and Giudici (2009), Wu et al. (2012a, b)
Kombucha vinegar	KV	1. *S. cerevisiae*; *S. codes ludwigii*; *S. bisporus*; 2. *C. stellata*; *C. guilliermondii*; 3. *Z. rouxii*; *Z. bailii*; *Z. kombuchaensis*; 4. *P. membranaefaciens*; 5. *Sc. pombe*; 6. *Rh. mucilagnosa*; 7. *Sm. ludwigii*; 8. *T. delbreuckii*	Kaur et al. (2011), Lončar et al. (2006), Malbaša et al. (2009), Sievers et al. (1995), Solieri and Giudici (2009), Sreeramulu et al. (2000), Steinkraus et al. (1996), Teoh et al. (2004)
Red vinegar	RV	1. *S. cerevisiae*; 2. *Ms. purpureus*; 3. *Rhodotorula* spp.	Solieri and Giudici (2009)
Vegetable vinegar			
Onion vinegar	OV	1. *S. cerevisiae*; *S. boulardii*; 2. *La. zymae*; *La. malefermentans*; *La. plantarum*; 3. *C. humilis*; 4. *Ka. exigua*	Cheng et al. (2014a, b), González Sáiz et al. (2008), Horiuchi et al. (1999, 2004; Vazirzadeh et al. 2012)
Tomato vinegar	TV	1. *S. cerevisiae*	Lee et al. (2013)
Fruit vinegar			
Fruit vinegar	FV	1. *S. cerevisiae*; 2. *Candida* sp.	Solieri and Giudici (2009)
Apple cider vinegar	ACV	1. *S. cerevisiae*; *S. uvarum*; 2. *Hs. uvarum*	Joshi and Sharma (2009)
Jujube vinegar	JV	1. *S. cerevisiae*	Vithlani and Patel (2010)
Coconut Vinegar	CNV	1. *S. chevalieri*; 2. *Kloeckera* spp.; 3. *C. pichia*; 4. *Tr. viride*	Muniswaran and Charyulu (1994), Okazaki et al. (2010), Solieri and Giudici (2009)
Mango vinegar	MV	1. *S. cerevisiae*; *S. cerevisiae* var. *bayanus*; 2. *Schizosaccharomyces* spp.	Akubor (1996), Ndoye et al. (2007), Sudheer Kumar et al. (2009)
Banana vinegar	BAV	1. *S. ellipsoideus*; *S. uvarum*; 2. *P. spartinae*	Krishna and Chandrasekaran (1996), Loesecke (1929)
Pineapple vinegar	PIV	1. *S. cerevisiae*	Sossou et al. (2009)
Cocoa vinegar	COV	1. *S. cerevisiae*; 2. *Kloeckera* spp.; 3. *Kl. marxianus*; 4. *P. fermentans*; 5. *Hs. uvarum*; *Hs. opuntiae*; 6. *Lo. elongisporus*; 7. *C. bombi*; 8. *Lb. fermentum*	Igbinadolor (2009), Illeghems et al. (2013)

Table 1 (continued)

Vinegar	Abbreviation	Strains	References
Cashew vinegar	CV	1. *S. cerevisiae*; *S. bayannus*	Garruti et al. (2006), Silva et al. (2007), Solieri and Giudici (2009)
Palm vinegar	PV	1. *S. cerevisiae*; *S. uvarum*; 3. *K. pichia*; 4. *Kl. lactis*; 5. *C. utilis*; *C. tropicalis*; *C. parapsilopsis*; *C. fermentati*; 6. *Sm. ludwigii*; 7. *Hs. uvarum*; 8. *Aspergillus* spp.; 9. *P. fermentans*; 10. *Lb. plantarum*; 11. *Le. mesenteroides*; 12. *Z. bailii*; 13. *Endomycopsis* spp.; 14. *Penicillium* spp.; 15. *Sc. pombe*	Amoa Awua et al. (2007), Solieri and Giudici (2009), Stringini et al. (2009)
Strawberry vinegar	STV	1. *S. cerevisiae*; 2. *Hs. uvarum*; 3. *Is. terricola*	Hidalgo et al. (2012c), Ubeda et al. (2012, 2013)
Sugarcane vinegar	SUV	1. *S. cerevisiae*	Kocher et al. (2006), Tzeng et al. (2009)
Persimmon vinegar	PEV	1. *S. cerevisiae*; 2. *D. anomala*; 3. *Me. pulcherrima*; 4. *P. guilliermondii*; 5. *Z. florentinus*; 6. *A. malorum*; 7. *H. uvarum*; 8. *Cryptococcus* sp.	Hidalgo et al. (2012a, b), Hwang et al. (2013)
Nata De Coco vinegar	NV	1. *S. cerevisiae*; 2. *Kloeckera* spp.; *3. Candida* sp.	Montealegre et al. (2012a, b), Solieri and Giudici (2009)
Balsamic vinegar	BV	1. *S. cerevisiae*	Solieri and Giudici (2009)
Traditional balsamic vinegar	TBV	1. *S. cerevisiae*; *S. ludwigii*; 2. *Hs. osmophila*; *Hs. valbyensis*; 3. *Z. mellis*; *Z. bisporus*; *Z. rouxii*; *Z. bailii*; *Z. pseudorouxii*; 4. *C. lactis-condensi*; 5. *C. stellata*	De Vero et al. (2006), Masino et al. (2008), Solieri et al. (2006, 2007), Solieri and Giudici (2008, 2009)
Wine vinegar			
Red wine vinegar	RWV	1. *S. cerevisiae*	Charles et al. (2000)
Malt/beer vinegar	M/BV	1. *S. cerevisiae*; *S. sensustricto*	Smogrovicova et al. (1997), Solieri and Giudici (2009)
Wine vinegar	WV	1. *S. cerevisiae*; *S. ludwigii*; 2. *H. uvarum*; 3. *C. stellata*; 4. *Ts. delbreuckii*; 5. *Lb. acetotolerans*; 6. *K. apiculata*	Ciani (1998), Li et al. (2011), Solieri and Giudici (2009)
Sherry/Jerez vinegar	S/JV	1. *S. cerevisiae*; *S. cerevisiae* var. *beticus*; *S. cerevisiae* var. *cheresiensis*; *S. cerevisiae* var. *montuliensis*; 2. *Z. rouxii*	Solieri and Giudici (2009), Tesfaye et al. (2009)
Animal vinegar			
Honey vinegar	HV	1. *S. cerevisiae*; 2. *Ts. delbreuckii*; 3. *Zygosaccharomyces* spp.	Dezmirean et al. (2012), Pereira et al. (2009), Solieri and Giudici (2009)
Whey vinegar	WHV	1. *S. cerevisiae*; 2. *Kl. marxianus*; *Kl. fragilis*; 3. *St. thermophilus*; 4. *Lb. delbrueckii*; *Lb. lactis*; *Lb. helveticus*; 5. *Cl. thermolacticum*	Dragone et al. (2009), Kourkoutas et al. (2002), Parrondo et al. (2009), Tamura (2000)

A. Acetobacter, *Ab. Absidia*, *As. Aspergillus*, *B. Brettanomyces*, *C. Candida*, *Cl. Clostridium*, *Cr. Cryptococcus*, *Ca. Caldicellulosiruptor*, *D. Dekkera*, *E. Endomycopsis*, *Eu. Eurotium*, *G. Gluconobacter*, *H. Hansenula*, *Hs. Hanseniaspora*, *Is. Issatchenkia*, *K. Kloeckera*, *Ka. Kazachstania*, *Kl. Kluyveromyces*, *Lb. Lactobacillus*, *Lo. Lodderomyces*, *Le. Leuconostoc*, *La. Lactococcus*, *M. Mucor*, *Ms. Monascus*, *Me. Metschnikowia*, *P. Pichia*, *Pc. Pediococcus*, *Pe. Penicillium*, *R. Rhizopus*, *Rh. Rhodotorula*, *S. Saccharomyces*, *Sa. Saccharum*, *Sc. Schizosaccharomyces*, *Sm. Saccharomycodes*, *Sp. Saccharomycopsis*, *Se. Saitoella*, *St. Streptococcus*, *T. Torulopsis*, *Ts. Torulospora*, *Tr. Trichoderma*, *W. Weissella*, *Z. Zygosaccharomyces*

fermentative metabolism and tolerance to ethanol. *S. cerevisiae* is known to be superior to non-*Saccharomyces* yeasts in the process of AF in spontaneous fermented wines (Sudheer Kumar et al. 2009; Wu et al. 2012a). For this reason, only a few osmotolerant species, such as *S. cerevisiae* and *S. cerevisiae* var. *bayanus*, can grow and metabolize well in some special vinegar fermentation conditions, such as high-temperature fermentation and high sugar concentration fermentation (Rainieri and Zambonelli 2009). Therefore, *S. cerevisiae* is the dominant yeast species involved in the AF stage of all vinegars, and it becomes dominant toward the end of AF. By contrast, non-*Saccharomyces* yeast species are particularly abundant during the initial and mid-AF stages of some vinegars. The large number of vinegar production enterprises in the world, with their unique ecological environments and diverse manufacturing procedures, results in typical "home microbiota" with a large diversity of microorganisms in vinegar. Specific yeasts and bacterial populations dominate

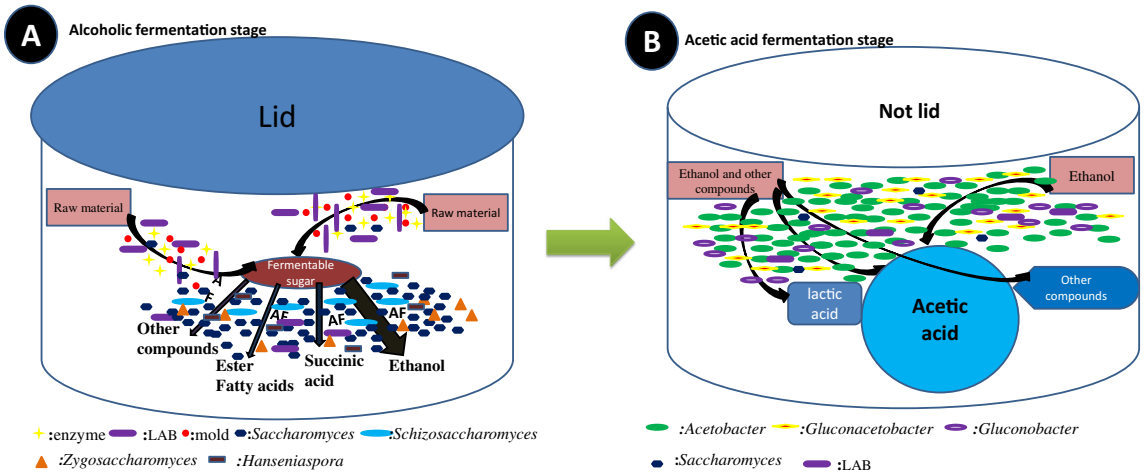

Fig. 2 **a**, **b** The microbial diversity involved in different fermentation stages

AF mainly because of the highly selective materials, operational conditions, and disparate sugar concentration and osmotic pressure, so the key species involved in AF of different types of vinegar vary (Wu et al. 2012a). Molds typically dominate the initial stages of AF because of their relatively rapid conversion of starch into sugar, followed by yeasts, in substrates that are rich in fermentable sugars. For example, the original rice material with a relatively low concentration of sugar mainly needs *Aspergillus* species to convert starch into fermentable sugars, and the metabolic activity from *Aspergillus* increases the sugar concentration. The genus *Saccharomyces* can rapidly consume low molecular weight sugar, thereby increasing the alcoholic degree. High alcoholic degree can inhibit the growth and metabolism of most other microorganisms. Therefore, the species isolated in AF of rice vinegar are mainly the genera *Saccharomyces* and *Aspergillus*. The dominant yeast species in AF of fruit vinegar are mainly the genus *Saccharomyces* because the fruit materials already have higher initial sugar concentration and do not need hydrolyzed starch. Given the differences in materials, species mainly from the genera *Lactobacillus* and *Saccharomyces* are isolated in the AF stage of animal vinegar. Moreover, the *Saccharomyces*, *Candida*, and *Lactobacillus* genera and most molds are present in AF of cereal vinegar, and the genus *Saccharomyces* is involved in AF of WV and vegetable vinegar (Table 1). For general vinegar production, the growth of lactic acid bacteria (LAB) in AF is not necessary and does not affect AAB activity, but LAB can affect the growth of yeasts and molds, which might significantly contribute to the quality of fermented vinegar (Li et al. 2014). For example, yeasts can only grow in whey or milk at pH 5, and this condition requires a lactic acid fermentation process carried out by LAB. Milk and whey are not ideal substrates for yeast growth because of their high pH and sugar composition, whereas LAB (e.g., *Lactobacillus* and *Streptococcus*) can lower pH in milk or whey vinegar fermentation (Rainieri and Zambonelli 2009). Therefore, LAB can also play a crucial role in early AF of milk or whey vinegar fermentation. Moreover, LAB populations also contribute a considerable content of lactic acid in vinegar, which can promote a soft taste by moderating the irritating sour smell (Chen et al. 2009). For example, among all the involved fermenting microorganisms, yeasts (*S. cerevisiae* and *Candida berkout*) and AAB (*Acetobacter indonesiensis*, *Acetobacter orientalis*, *Acetobacter senegalensis*, and *Acetobacter malorum*) are critical to the success of Shanxi aged vinegar (SAV) fermentation, whereas LAB (*Lactobacillus fermentum*, *Lactobacillus plantarum*, *Lactobacillus buchneri*, *Lactobacillus casei*) populations also make a great contribution to the taste of vinegar (Wu et al. 2012a). Nevertheless, LAB also can play a role in contributing to the acidization of swollen canned products (Cheng et al. 2014a).

In a nutshell, during vinegar production, the metabolic activities of yeasts and enzymes supplied by the action of molds play crucial roles in the AF stage (Wu et al. 2012a). Vinegar fermentation actually is a biological decomposition process that uses beneficial microorganisms as tools, and the main function of beneficial microorganisms in fermentation is using raw material as substrate to produce flavor compounds through metabolic activities.

Microbial diversity involved in acetic acid fermentation

Acetification is a biochemical process that requires microorganisms to oxidize ethanol into acetic acid under strict conditions of aerobiosis (Fig. 2). It has been traditionally considered as the most important process in vinegar production. Organic acids, including lactic acid and acetic acid, are the major sources of total acids and dominant flavor components of vinegar that are mainly produced during the AAF process (Nie et al. 2013; Tesfaye et al. 2002b). Previous studies showed that microbial communities in vinegar production

Table 2 Microorganisms isolated from acetic acid fermentation of different types of vinegar

Vinegar	Strains	References
Rice vinegar		
WRV	1. *A. pasteurianus*; *A. hansenii*; 2. *Ga. xylinus*; *Ga. europaeus*; 3. *Lb. acetotolerance*; *Lb. lactis*; 4. *Pc. Acidilactici*; 5. *Zy. mobilis*	Haruta et al. (2006), Okazaki et al. (2010), Solieri and Giudici (2009)
CRV	1. *Ga. xylinus*; 2. *A. pasteurianus*	Fu et al. (2013), Kawano et al. (2010)
BRV	1. *A. pasteurianus*; *A. aceti*; 2. *Ga. xylinus*; *Ga. europaeus*; *Ga. liquefaciens*; 3. *G. oxydans*; 4. *Lb. acetotolerance*	Hashimoto et al. (2013), Murooka and Yamshita (2008), Nanda et al. (2001), Solieri and Giudici (2009), Tokunaga et al. (2009)
ARV	1. *A. pasteurianus*; 2. *A. aceti*	Nanda et al. (2001), Solieri and Giudici (2009)
ZAV	1. *A. pomorum*; *A. pasteurianus*; 2. *Enterobacter* sp; 3. *Ps. geniculata*; *Ps. cissicola*; 4. *Lb. acetotolerans*; *Lb. gallinarum*; *Lb. crispatus*; *Lb. panis*; *Lb. pontis*; 5. *Ga. intermedius*; 6. *Flavobacterium* sp.; 7. *Sinorhizobium* sp; 8. *Sl. gallinarum*; *Sl. kloosii*	Xu et al. (2011a)
Cereal vinegar		
SV	1. *Acetobacter* spp.	Solieri and Giudici (2009)
C/GV	1. *A. pasteurianus*; *A. malorum*; *A. aceti*; *A. xylinum*; *A. liquefaciens*; *A. hansenii*; *A. rancens*; *A. tropicalis*; 2. *Ga. xylinus*; *Ga. europaeus*; 3. *Bacillus* spp.; 4. *Lactobacillus* spp.	Kawano et al. (2010), Solieri and Giudici (2009), Wu et al. (2010)
SAV	1. *A. pasteurianus*; *A. malorum*; *A. aceti*; *A. senegalensis*; *A. indonesiensis*; *A. orientalis*; *A. hansenii*; 2. *G. oxydans*; *Ga. hansenii*; *Ga. liquefaciens*; 3. *Lb. plantarum*; *Lb. casei*; *Lb. buchneri*; 4. *Pc. acidilactici*; *Pc. pentosaceus*	Solieri and Giudici (2009), Wu et al. (2012a, b)
KV	1. *A. xylinum*; *A. xylinoides*; *A. aceti*; 2. *Ba. gluconicum*; 3. *Ga. xylinus*; *Ga. intermedius*; *Ga. kombuchae*; 4. *Z. bailii*; 5. *Sc. pombe*; 6. *Ts. delbrueckii*; 7. *Rh. mucilaginosa*; 8. *Ko. rhaeticus*	Dos Santos et al. (2014), Kaur et al. (2011), Sievers et al. (1995), Solieri and Giudici (2009), Sreeramulu et al. (2000), Steinkraus et al. (1996), Teoh et al. (2004)
RV	1. *A. hansenii*; 2. *Ga. xylinus*	Solieri and Giudici (2009)
Vegetable vinegar		
OV	1. *A. aceti*; *A. pasteurianus*; *A. orientalis*	González Sáiz et al. (2008), Horiuchi et al. (1999), Horiuchi et al. (2004)
TV	1. *Acetobacter* spp.	Lee et al. (2013)
Fruit vinegar		
FV	1. *A. aceti*; *A. rancens*; *A. lovaniensis*; *A. xylinum*; 2. *Ga. xylinus*	Saeki et al. (1997), Solieri and Giudici (2009)
ACV	1. *A. pasteurianus*; *A. aceti*; *A. xylinum*; *A. pomorum*; *A. hansenii*; *A. oboediens*; *A. europaeus*; *A. syzygii*; 2. *Ga. xylinus*; *Ga. europaeus*; *Ga. hansenii*; *Ga. intermedius*	Fernández Pérez et al. (2010a), Hidalgo et al. (2012b), Sokollek et al. (1998b), Solieri and Giudici (2009)
JV	1. *A. xylinus*; *A. aceti*	Vithlani and Patel (2010)
CNV	1. *A. aceti*; *A. xylinum*	González and De Vuyst (2009), Solieri and Giudici (2009)
MV	1. *A. pasteurianus*; *A. aceti*; *A. lovaniensis*; *A. tropicalis*	Akubor (1996), Ndoye et al. (2006, 2007), Sudheer Kumar et al. (2009)
BAV	1. *Lb. acidophilus*	Tsen et al. (2003, 2004)
PIV	1. *A. aceti*; *A. pasteurianus*; *A. tropicalis*	Ou and Chang (2009), Sossou et al. (2009)
COV	1. *A. pasteurianus*; *A. tropicalis*; *A. senegalensis*	De Vuyst et al. (2008), Illeghems et al. (2013), Papalexandratou et al. (2011)
CV	1. *A. aceti*	Silva et al. (2007)
PV	1. *A. aceti*; 2. *Lb. plantarum*; 3. *Lc. mesenteriodes*; 4. *Zy. mobilis*	Solieri and Giudici (2009)
STV	1. *A. malorum*; 2. *Ga. saccharivorans*; *Ga. xylinus*	Hidalgo et al. (2012c)
SUV	1. *A. aceti*	Kocher et al. (2006), Kocher and Dhillon (2013)
PEV	1. *A. pasteurianus*; *A. malorum*; *A. cerevisiae*; *A. syzygii*; 2. *Ga. europaeus*; *Ga. intermedius*; *Ga. saccharivorans*	Hidalgo et al. (2012b), Hwang et al. (2013), Kim et al. (2006)

Table 2 (continued)

Vinegar	Strains	References
NV	1. *A. aceti*; *A. xylinum*; *A. hansenii*	Bernardo et al. (1998), Montealegre et al. (2012b), Santosa et al. (2012), Solieri and Giudici (2009)
BV	1. *A. hansenii*	Chen et al. (2010)
TBV	1. *A. pasteurianus*; *A. malorum*; *A. aceti*; *A. hansenii*; *A. pomorum*; 2. *Ga. xylinus*; *Ga. europaeus*; *Ga. hansenii*; *Ga. azotocaptans*; *Ga. diazotrophicus*; *Ga. liquefaciens*; *Ga. oboediens*; *Ga. sacchari*; *Ga. oxydans*; *Ga. cerinus*	De Vero et al. (2006), Gullo et al. (2006), Gullo et al. (2009), Gullo and Giudici (2008), Masino et al. (2008), Solieri and Giudici (2009), Solieri et al. (2006)
Wine vinegar		
RWV	1. *A. pomorum*; *A. oboediens*; 2. *Ga. europaeus*	Fernández Pérez et al. (2010b), Sokollek et al. (1998a), Solieri and Giudici (2009)
M/BV	1. *A. cerevisiae*; 2. *Ga. sacchari*; *Ga. europaeus*	Solieri and Giudici (2009)
WV	1. *A. pasteurianus*; *A. aceti*; *A. xylinum*; *A. pomorum*; *A. liquefaciens*; *A. hansenii*; *A. methanolicus*; *A. diazotrophicus*; *A. polyoxogenes*; 2. *G. oxydans*; *G. oxydans* subsp. *sphaerricus*; *Ga. xylinus*; *Ga. europaeus*; *Ga. hansenii*; *Ga. intermedius*; *Ga. oboediens*; *Ga. entanii*; *Ga. pomorum*; 3. *S. cerevisiae*	Ciani (1998), Fregapane et al. (1999), Hidalgo et al. (2010), Solieri and Giudici (2009); Tesfaye et al. (2002a, b, c), Vegas et al. (2010, Vegas et al. 2013)
S/JV	1. *Acetobacter* spp.; 2. *Gluconobacter* spp.	Palacios et al. (2002)
Animal vinegar		
HV	1. *Acetobacter* spp.; 2. *Gluconacetobacter* spp.	Solieri and Giudici (2009)
WHV	1. *A. pasteurianus*; 2. *Ga. liquefaciens*	Parrondo et al. (2003), Solieri and Giudici (2009)

A. Acetobacter, *B. Bacillus*, *Br. Brettanomyces*, *Ba. Bacterium*, *Eb. Enterobacter*, *F. Flavobacterium*, *G. Gluconobacter*, *Ga. Gluconacetobacter*, *Ko. Komagataeibacter*, *Lb. Lactobacillus*, *Lc. Leuconostoc*, *Pc. Pediococcus*, *Ps. Pseudomonas*, *Rh. Rhodotorula*, *S. Saccharomyces*, *Sc. Schizosaccharomyces*, *Sl. Staphylococcus*, *Si. Sinorhizobium*, *Ts. Torulospora*, *W. Weissella*, *Z. Zygosaccharomyces*, *Zy. Zymomonas*

are comparatively stable, but microbial diversity undergoes a series of regular changes during different fermentation processes (Xu et al. 2011a). Thus, the dynamic changes in a microbial community during AAF are different from those during other fermentation stages (Nie et al. 2013). For this reason, a summary of microbial diversity and function in AAF of different types of vinegar is urgently needed.

Most AAB are capable of oxidizing ethanol as substrate to acetic acid in neutral and acidic (pH 3.0–4.0) media (Gullo and Giudici 2008; Schüller et al. 2000; Sokollek et al. 1998b), and they are the main oxidative microorganisms able to survive in high ethanol and high acidic conditions, such as in wine and vinegar (González et al. 2005). High alcohol concentrations at the initial stage of acetification, as well as high acidic conditions at the middle and late stages of AAF, suggest that most of the bacteria present are AAB (Hidalgo et al. 2012a). Microorganisms isolated from AAF of different types of vinegar are displayed in Table 2. Various kinds of raw materials are used as substrate, different types of starter cultures are used in fermentation, and disparate physicochemical properties are needed in vinegar production. All these factors lead to microbial diversity in AAF of vinegar production. Most bacteria present in the AAF stage belong to the genera *Acetobacter*, *Gluconacetobacter*, and *Gluconobacter*. Previous studies revealed that only two genera of AAB are mainly involved in AAF of vinegar production, namely, *Gluconobacter* and *Acetobacter* (García García et al. 2009; Maal et al. 2010; Sokollek et al. 1998a; Tesfaye et al. 2002b). However, current research indicated that some species of *Gluconacetobacter* also possess the ability to oxidize ethanol into acetic acid under high alcohol concentrations and high acidity conditions (Hidalgo et al. 2012a; Lisdiyanti et al. 2006). For example, *Gluconacetobacter saccharivorans* can oxidize ethanol at high alcohol concentration (more than 11.5 % (*v*/*v*)) (Kato et al. 2011). *Acetobacter* oxidizes ethanol more strongly than glucose, and its main function is to oxidize ethanol to acetic acid (Tesfaye et al. 2002b). By contrast, the *Gluconacetobacter* genus is known to have a higher tolerance to acetic acid than *Acetobacter*. Moreover, the *Acetobacter* genus has always been associated with traditional WV fermentation, while *Gluconacetobacter* species are linked with vinegar production in submerged systems, where the conditions are more extreme. Therefore, *Acetobacter* species are abundant during the initial and mid-AAF stages, whereas *Gluconacetobacter* species are dominant during the final stages of AAF (Hidalgo et al. 2012a). Unlike *Acetobacter* and *Gluconacetobacter* species, *Gluconobacter* bacteria oxidize glucose more strongly than ethanol, and their main

role is the oxidation of glucose to gluconic acid (Tesfaye et al. 2002b). Hence, *Gluconobacter* bacteria are involved in two fermentation stages (AF and AAF), and they can continue to convert glucose into gluconic acid and ethanol under high alcohol and acidity conditions. However, the genera *Acetobacter* and *Gluconacetobacter* are mainly involved in AAF step, and they mainly oxidize ethanol into acetic acid. These characteristics also explain why *Gluconobacter* species are always involved in early acetification, which still contains a certain amount of glucose. By contrast, the genera *Acetobacter* and *Gluconacetobacter* are involved in all AAF stages. However, numerous studies indicated that the primary bacteria existing during the AAF process belong to the genus *Acetobacter* (Haruta et al. 2006; Nanda et al. 2001; Xu et al. 2011a).

In addition to those described above for the AAB genus, a new genus *Komagataeibacter* has been proposed, and most species of this genus are transferred from the genus *Gluconacetobacter* (Yamada et al. 2012). Some *Komagataeibacter* species are also involved in industrial vinegar fermentation, and they are the most resistant Acetobacteraceae family to high acetic acid concentrations, such as *Komagataeibacter xylinus*, *Komagataeibacter hansenii*, *Komagataeibacter europaeus*, *Komagataeibacter saccharivorans*, *Komagataeibacter nataicola*, and *Komagataeibacter intermedius* (Suwanposri et al. 2014; Yamada et al. 2013). The *Komagataeibacter* species can also produce acetic acid from ethanol. Their growth and metabolism are positive in the presence of acetic acid, and they can oxidize acetate and lactate to water and carbon dioxide (Yamada et al. 2012). In some *Komagataeibacter* species, cellulosic materials are produced, whereas acetic acid is required for growth in some species (Dos Santos et al. 2014; Suwanposri et al. 2014; Yamada et al. 2012). Given the unique features and functions of the genus *Komagataeibacter*, *Komagataeibacter* species also play an important role in AAF of vinegar production.

Some studies demonstrated that the greatest hurdle to AAB growth is the high sugar concentration (Gullo et al. 2006), and the AF stage has high sugar concentration through starch saccharification, so only few AAB are present in the AF stage. However, considering the high acidity conditions at the middle and late stages of AAF, as well as the decreased concentration of sugar caused by the conversion of sugar to ethanol, most of the bacteria involved in AAF are AAB (Hidalgo et al. 2012a). At present, acetification of vinegar is becoming increasingly carried out with mixed and often undefined cultures, so not only AAB can be isolated in AAF. For example, the bacteria existing during AAF of Zhenjiang aromatic vinegar also include *Lactobacillus*, *Enterobacter*, *Staphylococcus*, *Flavobacterium*, *Pseudomonas*, and *Sinorhizobium* species (Table 2) (Xu et al. 2011a).

Physicochemical properties and compounds in different types of vinegar

Aroma components play an important role in the quality of vinegar, so understanding the major aroma components present in different types of vinegar is necessary. The main methods, namely, chemical analysis, electronic nose, and sensory analysis, are used to measure the aroma components in vinegar (Zhang et al. 2008). Several studies indicated that chemical analysis plays a major role in component analysis, such as high-performance liquid chromatography (HPLC) and gas chromatography-mass spectrometry (GC-MS), which are always used to evaluate the key compounds of vinegar (Chinnici et al. 2003; Consonni et al. 2008; Durán Guerrero et al. 2008; Lu et al. 2011; Peng et al. 2009). The important metabolites are analyzed by HPLC (Cheng et al. 2014a), and volatile compounds are mainly analyzed by headspace solid-phase microextraction GC-MS (Pollien et al. 1997). With these analytical methods, a link can be made between the metabolites, substrates, and microbes identified (Cheng et al. 2014a, b). In addition, pyrolysis MS and nuclear magnetic resonance spectroscopy are always conducted to distinguish representative compounds of well-known flavor types of vinegar (Anklam et al. 1998; Caligiani et al. 2007; Jo et al. 2013; Zhang et al. 2008). The physicochemical properties, concentrations of organic acids, content of polyphenols, and levels of other compounds in different types of vinegar are presented in Tables 3 and 4. In the qualitative analysis of vinegar, large numbers of organic acids and polyphenols are selected as discriminant variables (Gálvez et al. 1994; Natera et al. 2003). However, most volatile short-chain organic acids affect the flavor, quality, and acidity of vinegar. These volatile acids are mainly acetic acid, butyric acid, and smaller propionic acid, which all come from raw materials or are generated during fermentation (Sossou et al. 2009). Therefore, the analysis and summary of final physicochemical properties and compounds in different types of vinegar are critical to the appraisal of vinegar quality.

Understanding the contribution of physicochemical parameters to microbial diversity and vinegar aroma quality is urgent. In AAF, the important physicochemical parameters that affect the growth of microorganisms are pH and acidity (Ghosh et al. 2012). At lower pH of vinegar, the growth of most microorganisms is believed to be inhibited. For instance, acetic acid has strong antibacterial activity at low pH, so vinegar with high acidity has a better inhibitory effect on vinegar spoilage. By contrast, moderately acidic vinegar has been revealed to retain most sensory odors and volatile compounds (Jo et al. 2013). Consequently, to guarantee the quality of vinegar, we should control the physicochemical parameters at suitable values. As shown in Table 4, acidity in the balsamic vinegar (BV) is higher than that in TBV, whereas the concentrations of most volatile and aroma compounds in BV are

Table 3 Compounds in different types of vinegar

Vinegar	Acetic acid[a]	Lactic acid[b]	Citric acid[b]	Malic acid[b]	Succinic acid[b]	Gallic acid[b]	Tartaric acid[b]	Acetoin[b]	Ethanol[c]	References
Rice vinegar										
WRV	3.5–7.43	20.3–214	2.09	0.52	14.1–32	1.68–2.14	nd	251	0.68	Bunick et al. (2012), Caligiani et al. (2007), Nishidai et al. (2000)
CRV	3.44–6.8	67.8–328.6	29.48–94.07	27.38–97.66	10.14–27.66	nd	135–240	63.1	nd	Lee et al. (2012), Li et al. (2014), Zhang et al. (2008)
ZAV	3.48–5.32	712.2–3385	5.6	1.9	26.4	nd	135.3	nd	nd	Lu et al. (2011), Xu et al. (2011a, b)
Cereal vinegar										
SV	2.3–2.5	nd	nd	nd	nd	7.58	nd	nd	19.7–23.1	Fan et al. (2009)
C/GV	3.59	nd	273	nd	nd	2.13	nd	nd	nd	Nishidai et al. (2000), Ye et al. (2004)
SAV	3.6–4.3	nd	60–150	760–1550	36–62	nd	400–970	96.3–237.8	0.0281	Chen et al. (2010), Cocchi et al. (2006)
RV	4–5	nd	nd	nd	nd	nd	nd	1.7–2.0	nd	Bunick et al. (2012), Chen and Xu (2010)
Vegetable vinegar										
OV	2.07–3.79	6	98.7	47.5	24.1	nd	6.4	nd	0.04–0.2	Hidalgo Albornoz (2012), Horiuchi et al. (1999), Horiuchi et al. (2004)
TV	3.85–5.73	164	1860	364	79	nd	nd	56	0.16	Caligiani et al. (2007), Lee et al. (2013)
Fruit vinegar										
FV	1.8–2.6	43.59–64.11	166.3	202.4–285.7	29.31–241.38	2.85–3.26	16.67–218	nd	nd	Cerezo et al. (2008), Lin et al. (2011), Ubeda et al. (2011a, b)
ACV	3.07–5.67	3.6–202	18–95	6.53–8.6	11.9–27	0.402	6.47	20.6–21	0.03–2.0	Budak et al. (2011), Bunick et al. (2012), Caligiani et al. (2007), Horiuchi et al. (1999)
PV	1.08–6.81	55.1	29.41	18.18	9.09	nd	8.82	nd	0.5	Lin et al. (2011)
BV	5.49–6.25	49–124	35–188	360–1160	40–78	6.45	158–255	37–58	0.06–0.234	Bunick et al. (2012), Caligiani et al. (2007), Del Signore (2001), Hillmann et al. (2012)
TBV	4.66–5.35	43–91	83–200	703–992.7	50.12–104	nd	304–506	32–487.5	0.01–0.053	Caligiani et al. (2007), Del Signore (2001), Hidalgo Albornoz (2012)
Wine vinegar										
RWV	5–8.97	20.06–103	14.04–40.2	12.79–33.7	21.98–39.8	1.8–4.61	59.6–220	6–36.4	1.33	Bunick et al. (2012), Cerezo et al. (2010a, b), Charles et al. (2000), Giumanini et al. (2001)
M/BV	4.3–6	40.3–149	0.69	0.06	2.85–30	0.53	nd	20–102	0.05–0.20	Bunick et al. (2012), Caligiani et al. (2007), Horiuchi et al. (1999)
WV	5–7.89	5.5–76	9–61	20.3–66	8.1–55	1.04–3.68	91–300	39.2–61	0.6–2	Caligiani et al. (2007), Horiuchi et al. (1999), Morales et al. (2004), Sáiz Abajo et al. (2006), Tesfaye et al. (2004), Tesfaye et al. (2002a, b, c)

Table 3 (continued)

Vinegar	Acetic acid[a]	Lactic acid[b]	Citric acid[b]	Malic acid[b]	Succinic acid[b]	Gallic acid[b]	Tartaric acid[b]	Acetoin[b]	Ethanol[c]	References
S/JV	7.4–11.17	200–347	24–195	16–34	56–332	0.57–1.17	185–385	39.2–68	0.09–2.2	Bunick et al. (2012), Cejudo Bastante et al. (2012), Hidalgo Albornoz (2012), Morales et al. (2001a, b), Morales et al. (2002)
Animal vinegar										
HV	6.76	111	9.3–21	51.5	27.3	0.326	21.2–47.78	nd	nd	Küçük et al. (2007), Natera et al. (2003), Viuda Martos et al. (2010)

nd not detected

[a] Expressed as grams/100 mL, *w/v*

[b] Expressed as milligrams/100 mL

[c] Expressed as percent, *v/v*

lower than those in TBV (Table 3). Compared with BV, TBV has more moderate acidity, so it is more conducive to the quality of vinegar.

The volatile and nonvolatile compounds involved in vinegar production are important to the aromatic quality and antioxidant activity of vinegar. Kurosu is one of the most famous traditional healthy vinegars in Japan, and it is characterized by higher levels of organic acids and amino acids than other vinegars (Murooka and Yamshita 2008; Nagashima and Saito 2010). Kurosu has been found to exhibit higher levels of antioxidant activity than cereal/grain vinegar (C/GV), Komesu, white rice vinegar (WRV), TBV, WV, and most fruit vinegar. Such levels of antioxidant activity are due to the fact that Kurosu contains higher concentrations of 2,2-diphenyl-1-pycrylhydrazyl (DPPH) radical scavenging compounds compared with other vinegars. The dihydrosinapic acid (DSA) and dihydroferulic acid (DFA) are DPPH radical scavenging compounds that have been found in the nonvolatile acidic part of Kurosu. DSA and DFA are the homologues of sinapic acid and ferulic acid, respectively, which are known as natural antioxidants in unpolished rice, wheat, rice, and other grains. Moreover, the levels of antioxidative activity of DSA and DFA are stronger than those of their homologues, sinapic acid and ferulic acid. The concentrations of DSA and DFA are lower in common rice vinegar (polished rice vinegar), but higher in Kurosu, so Kurosu is more advantageous than polished rice vinegar as an antioxidative food item (Shimoji et al. 2002). In addition, the presence of phenolic compounds can significantly affect the aromatic quality (Qingping 2006), and several papers suggested that phenolic compounds also play a key role in the antioxidant activity of vinegar (Cejudo Bastante et al. 2010; Xu et al. 2007).

Fermentation methods in vinegar production

In terms of technological processing, the main biotechnological process and fermentation methods involved in vinegar production are carried out in the AAF stage (Ndoye et al. 2007). From technological aspects, two well-defined methods can be used for vinegar production: submerged (quick) methods and traditional (slow) processes (Tesfaye et al. 2002b). Vinegar production is actually a process of microbial fermentation, and microbial fermentation can be induced either by three methods: spontaneous fermentation, backslopping fermentation, and starter culture fermentation (Solieri and Giudici 2009). The production of traditional Chinese rice vinegar mainly include solid-state fermentation, deep liquid fermentation, and surface fermentation (Fu et al. 2013; Liu et al. 2004). The primitive vinegar fermentation method is spontaneous fermentation. In this method, the changed environmental conditions and raw material encourage growth of the most appropriate indigenous microbial communities.

Table 4 The physicochemical properties in different types of vinegar

Vinegar	Major raw material	TPI[a]	DPPH[b]	TAA[c]	Acidity[d]	pH	Total ash[a]	Color	References
Rice vinegar									
WRV	Rice	64	nd	133	3.5–5.0	1.71–3.5	nd	White	Liu et al. (2008a), Okazaki et al. (2010), Ye et al. (2004), Zhang et al. (2006)
CRV	Brown rice/wheat/sorghum	nd	nd	700	4.32–6.06	1.71–3.51	nd	Black/amber	Li et al. (2014), Liu et al. (2008a), Zhang et al. (2008), Zhang et al. (2006)
BRV	Unpolished black rice	73.3–112	294	nd	nd	nd	nd	Dark brown/black	Ghosh et al. (2012), Hidalgo Albornoz (2012), Nishidai et al. (2000), Sakanaka and Ishihara (2008), Shimoji et al. (2002)
ARV	Polished amber rice	nd	238	nd	nd	3.1	nd	Amber	Ghosh et al. (2012), Murooka and Yamshita (2008), Nanda et al. (2001), Shimoji et al. (2002)
ZAV	Sticky rice	nd	nd	1100	6.0–6.25	3.8–4.0	nd	Amber	Hidalgo Albornoz (2012), Xu et al. (2011a), Zhang et al. (2006)
Cereal vinegar									
SAV	Mille/buckwheat/ barley/sorghum/bran	nd	nd	2300	4.5–6	3.85–4.15	nd	Black purple	Cocchi et al. (2006), Zhang et al. (2006)
KV	Tea and sugar	nd	nd	nd	4.2–5.11	2.4–3.75	nd	Light orange	Kaur et al. (2011), Sievers et al. (1995)
Vegetable vinegar									
OV	Onion	nd	nd	210	nd	3.67–3.89	nd	Red	Horiuchi et al. (2000a, b)
Fruit vinegar									
FV	Fruit	nd	nd	nd	2.5	2.9–3.7	nd	Brown	Liu et al. (2008b, 2011), Zhang et al. (2006)
ACV	Apple	41.7–90.86	203.6	6.6–217	5.52–7.38	2.83–3.8	105–500	Light amber	Nakamura et al. (2010), Natera et al. (2003), Nishidai et al. (2000)
JV	Red date	45.75	76.49	nd	3.96	3.14	nd	Red	Vithlani and Patel (2010)
MV	Mango	nd	nd	nd	8–9	3.1–5.1	300–820	Black/yellow	Akubor (1996), Zhu et al. (2003)
PIV	Pineapple	nd	nd	nd	0.25–7.16	2.9	nd	Red-brown	Ou and Chang (2009), Sossou et al. (2009)
COV	Cocoa beans	nd	nd	nd	nd	3.6	400–500		Igbinadolor (2009)
CV	Cashew	nd	nd	420	nd	3.8	455		Igbinadolor (2009), Zhang et al. (2006)
STV	Strawberry	69.4–78.1	321–339	nd	nd	nd	nd	Red-brown	Ubeda et al. (2013)
SUV	Sugarcane	nd	nd	nd	4.2–6.7	2.4	nd	Brown	Kocher et al. (2006)
PEV	Kaki	27.32–79.9	145–173	nd	nd	nd	nd	Brown red	Sakanaka and Ishihara (2008), Ubeda et al. (2011a, b)
BV	Cooked grape must	253.9	nd	nd	6.82–10	3.5–3.73	nd	Modena	Consonni and Cagliani (2007), Consonni et al. (2008)

Table 4 (continued)

Vinegar	Major raw material	TPI[a]	DPPH[b]	TAA[c]	Acidity[d]	pH	Total ash[a]	Color	References
TBV	Cooked grape must	nd	nd	nd	7.8–8.5	2.22–4.26	500–600	Dark brown	Antonelli et al. (2004), Giudici et al. (2009), Masino et al. (2008)
Wine vinegar									
RWV	Grape	100.6–192	122.9	nd	5–6	3–3.06	nd	Red	Bunick et al. (2012), Cerezo et al. (2008, 2010a, b), Hidalgo Albornoz (2012), Natera et al. (2003)
M/BV	Malted barley	nd	nd	48.1	5–6	nd	nd	Straw-colored/dark brown	Grierson (2009), Hidalgo Albornoz (2012), Jones and Greenshields (1969), Xu et al. (2011a, b)
WV	Grape	71.3–175	93.9	18.91–77	4–6	2.8–3.4	106–110	Brown	Cerezo et al. (2010a, b), Ciani (1998), Hidalgo Albornoz (2012), Hidalgo et al. (2010), Kutlán and Molnár Perl (2003), Nishidai et al. (2000), Sellmer Wilsberg (2009), Vegas et al. (2010)
S/JV	Grape	31–51.2	206.6	73–123.5	6–11.4	2.6–2.9	380–1810	Red-brown	Morales et al. (2001a, b), Palacios et al. (2002), Parrilla et al. (1999), Tesfaye et al. (2002a, c)
Animal vinegar									
HV	Honey	nd	nd	9–21	nd	3.63–4.9	nd	Amber	Dezmirean et al. (2012), Natera et al. (2003), Viuda Martos et al. (2010)

TPI total phenolic index, *DPPH* 2,2-diphenyl-1-pycrylhydrazyl, *TAA* total amino acid, *nd* not detected

[a] Expressed as milligrams of gallic acid/100 g

[b] Expressed in micromoles of TE/100 g

[c] Expressed as grams/100 mL, *w/v*

[d] Expressed as milligrams/100 mL

Furthermore, the more stringent the growth conditions are, the greater the selective pressure exerted on the indigenous microorganisms (Solieri and Giudici 2009). Natural vinegar made from different sources of derived ethanol (such as cider, beer, wine, and fermented fruit juice) by spontaneous fermentation methods not only contains small amounts of citric acid, tartaric acid, and other organic acids, but also require a long fermentation time (Ghosh et al. 2012). To increase the speed of the biological reaction, the dominant AAB are used in the aerobic transformation of ethanol into acetic acid, and various fermentation methods have been developed (De Ory et al. 2004; Tesfaye et al. 2002b). Although many diverse fermentation methods are applied in vinegar production, most fermentation methods involved in industrial vinegar production are modified methods, and all of them are based on the submerged culture method (Arnold et al. 2002; Fregapane et al. 2001). Generally, industrial vinegar is produced by two main methods. One is a slow process involving static surface acetic acid fermentation and traditional surface fermentation; these methods comprise the so-called surface culture fermentation, where the AAB are placed on the air-liquid interface for direct contact with oxygen (Tesfaye et al. 2002b). The other is the quick submerged fermentation process involving continuous submerged culture and semicontinuous acetic acid fermentation. For example, static surface acetic acid fermentation is employed in traditional vinegar production such as Komesu and Kurosu. This technique is not costly in terms of plant investment, and the quality of the final product is superior, although a rather long time is required to complete fermentation (Table 5) (Haruta et al. 2006). In most modern industrial vinegar production units, the submerged fermentation process is the main method used (Arnold et al. 2002; Baena Ruano et al. 2006); however, semicontinuous acetic acid fermentation is currently one of the most common fermentation methods in vinegar production (De Ory et al. 2004). Furthermore, different from submerged pure culture fermentation techniques for vinegar production in European countries (Tesfaye et al. 2002b), solid or semisolid mix culture fermentation techniques are widely used in Asian countries (Xu et al. 2011a). In particular, Chinese vinegars and cereal vinegars are mostly produced by a typical aerobic solid-state fermentation (SSF) (Wu et al. 2010; Xu et al. 2011a). SSF refers to the growth of microbes on moist solid substrate without free-flowing water. SSF processes may be more practical and suitable than deep liquid fermentation for low-technology applications (Table 5). This fermentation method is widespread in Asian countries to produce vinegar at a small scale (Wu et al. 2010), whereas China uses this method on a large scale for vinegar production (Liu et al. 2004).

In addition to the aforementioned fermentation methods, other important liquid culture methods, such as shake-flask fermentation and stationary surface culture fermentation, are also applied in vinegar production (Table 5). To determine the optimal conditions of vinegar production, such as quality of vinegar, capital investment, and operating cost, diverse fermentation methods are used for vinegar production. For instance, WV is mainly produced in Mediterranean countries, and different fermentation methods have been used to improve the quality of WV. The traditional surface fermentation method of WV production usually acquires high value because of its outstanding sensory properties, but production requires maturation in wood for several years to obtain a high acetic degree; thus, the finished product is relatively valuable (Charles et al. 2000). To overcome this difficulty, new fermentation methods have been designed, such as submerged liquid culture, deep liquid fermentation, and a continuous aeration system (Tesfaye et al. 2002b).

Relationship between microbial diversity and other determinant factors

The final quality of vinegar is determined by many factors, in which the microbial diversity involved in vinegar fermentation and the raw materials may be the major determinant factors, because vinegar's physicochemical parameters and chemical composition are mainly influenced by these factors (Morales et al. 2001b). All of the factors are closely related to each other, and they all affect the vinegar fermentation process (Morales et al. 2001b; Natera et al. 2003). Furthermore, the quality of vinegar is also strongly determined by sensory properties as it may modify the overall quality of a given food or meal, and the sensory properties are mainly determined by metabolism of microorganisms. Studies have now highlighted that the metabolism of microorganisms can affect vinegar chemical properties in a remarkable way (Li et al. 2014, 2015).

The odorant compounds play a vital role in vinegar's flavor (Castro Mejías et al. 2002; Tesfaye et al. 2002b). For example, Zhenjiang aromatic vinegar (ZAV) and SAV are two typical types of famous China-style vinegars, and they are famous all over the world because of their unique flavor, which is the result of different concentrations of aroma compounds (Table 3) (Aili et al. 2012; Lu et al. 2011). Moreover, the final composition of vinegar is also influenced by the raw material and fermentation methods used in the process, and both of these factors can lead to microbial differences in fermentation. For instance, Cantonese-style rice vinegar is famous in China for its high acidity and special fragrance because special acidogenic bacteria are used as starter culture, brown rice is selected as the raw material, and surface acetic acid fermentation method is used for fermentation (Fu et al. 2013). In addition, SAV is produced from barley, mille, wheat, bran, sorghum, and buckwheat by spontaneous fermentation and SSF. More than 45 compounds are detected in SAV, of which 13 compounds have not been previously reported in other

Table 5 Different fermentation methods in vinegar production

Fermentation method	Advantages	Disadvantages	RV	References
Fermentation can be induced by three methods				
Spontaneous fermentation	Suitable for small-scale production; without the use of starter culture; a cheap and simple traditional fermentation method	Low efficiency of the process and long fermentation time; only suitable for very specific juices. Difficult to control and there is a great risk of spoilage to occur.	SUV SAV PV	Ghosh et al. (2012), Kocher et al. (2006), Mimura et al. (2004), Solieri and Giudici (2009), Wu et al. (2012b)
Starter culture fermentation	It increases the safety, the stability, and the efficiency of the process; it reduces production losses caused by uncontrolled fermentation, eliminating undesired features; shortens the fermentation process and reduces the risk of fermentation failure.	Starter cultures are not very flexible with regard to the desired properties and functionality of the end product.	TBV PV	Ghosh et al. (2012), Gullo et al. (2009), Leroy and De Vuyst (2004), Solieri and Giudici (2009)
Back-slopping fermentation	More reliable, cheaper, and faster process than spontaneous fermentation; reduces spoilage from occurring. The risk of fermentation failure is reduced.	Still has the risk of spoilage to occur; the initial phase of the fermentation process is shortened.	TBA WV CRV	Holzapfel (2002), Leroy and De Vuyst (2004), Solieri and Giudici (2008), Solieri and Giudici (2009), Viiard et al. (2013)
Main fermentation methods of traditional Chinese vinegar				
Deep liquid fermentation	Quick fermentation method; fast oxidation of alcohol and greater efficiency is achieved; the ratio of productivity to capital investment is much higher; the process can be highly automated.	The metabolisms of microorganisms are lower than solid-state fermentation; produces higher wastewater than solid-state fermentation; a smaller reactor is needed.	CRV WV ACV	Baena Ruano et al. (2006), Charles et al. (2000), Fernández Pérez et al. (2010b), Fu et al. (2013), Solieri et al. (2007), Viniegra González et al. (2003)
Solid-state fermentation	Low-technology applications: cheap unrefined agricultural products are used as substrates, capital investment and operating cost are moderate, aseptic processing is less stringent; solid-state processes have lower energy requirements; produces lesser wastewater and is environmental-friendly as it resolves the problem of solid wastes disposal; higher productivity; it resembles the natural habitat for several microorganisms.	Difficulties on scale-up; difficult control of process parameters; low mix effectively; the time required and the inability to detect viable but nonculturable bacteria; the growth time of the active microorganisms involved in this bioprocess is too long.	C/GV SAV ZAV	Baena Ruano et al. (2006), Chen et al. (2009), Couto and Sanromán (2006), Hölker and Lenz (2005), Liu et al. (2004), Lu et al. (2011), Pandey (2003), Thomas et al. (2013), Wu et al. (2010), Xu et al. (2011a)
Traditional surface fermentation	Obtains high-quality vinegar	Slow fermentation method: long period of time is required to obtain a high acetic degree	CRV RWV S/JV	Callejón et al. (2009), Cerezo et al. (2010a), Charles et al. (2000), Fu et al. (2013), Morales et al. (2001a)
From a technological point of classification				
Stationary surface culture	The brewed vinegar obtained is superior in quality; the production can be practised with a very simple apparatus; organic acid content is higher than agitated culture.	Takes a long period of time to ferment; the yield of the product vinegar or the utilization rate of the starting material is low.	BRV ARV C/GV FV	Hashimoto et al. (2013), Lee et al. (2012), Nanda et al. (2004), Nanda et al. (2001)
Shake-flask fermentation	Obtains high concentrations of volatile compounds; beneficial to solve oxygen limitation	Obtains low concentrations of organic acids	CRV	Fang and Zhong (2002), Fu et al. (2013), Lee et al. (2012)
Semicontinuous acetic acid fermentation	Higher acetification rates; obtains high total and volatile acidity; the method is quicker and easier.	Higher evaporative losses of volatile compounds	MV KV WV	Adams (1985), De Ory et al. (2004), Fregapane et al. (2001), Fregapane et al. (1999), Kaur et al. (2011), Ndoye et al. (2007)
Continuous submerged culture	High fermentation rate and yield of acetic acid	Requires precise control of fermentation for efficient vinegar production	ACV	Budak et al. (2011)

RV representative vinegar

vinegars. SAV differs from other vinegars because of its unique thermal process (6 days at 85 °C), special raw materials, and diverse fermentation methods, which create its typical aroma compounds (Aili et al. 2012). The fermentation methods are also important for the functions of vinegar. ACV produced with maceration in the surface method has high total phenolic content, ORAC levels, chlorogenic acid, and TEAC, which exert positive effects on delaying gastric emptying and lowering postprandial blood glucose and insulin levels, liver functions and steatosis, body weight increase, and blood lipid levels (Budak et al. 2011; Hlebowicz et al. 2007).

The relationship between microbial diversity and raw materials

To date, various types of vinegar are produced with different types of raw materials. The main raw materials for Chinese vinegar production are cereals and their bran. However, many other sugar-containing and starch materials, such as fruits and sweet potato, have found their way into vinegar production (Liu et al. 2004). Furthermore, the main difference between European vinegar and Chinese vinegar is the raw materials used. European vinegar is usually produced from cider, wine, malted barley, fruit honey, pure alcohol, or juices, whereas Chinese vinegar is always produced from wheat bran, rice, and sticky rice as raw materials (Castro Mejías et al. 2002; Lipp et al. 1998; Zhang et al. 2006).

In vinegar fermentation, the selection, preparation, and fermentation of raw materials are crucial because one of the most possible causes of strain diversity in AF and AAF can be the effect of raw material composition (Wu et al. 2010). The chemical composition of a raw material exerts a very strong selective pressure on microorganisms and determines the dominant species involved in saccharification, liquefaction, AF, and acetification. As shown in Table 1, vinegar production with different raw materials results in obvious strain diversity in AF. For instance, given that cereal materials contain more starch but less sugar, yeasts and molds are mainly responsible for AF in cereal vinegar fermentation (Li et al. 2014), and the dominant strains in AF of cereal vinegar are mainly *Saccharomyces*, *Lactobacillus*, *Aspergillus*, *Mucor*, and *Rhizopus* species. Compared with fruit vinegar, significantly more *Aspergillus*, *Mucor*, and *Rhizopus* species are involved in cereal vinegar's initial stages of AF. This phenomenon is mainly due to the fact that molds are the dominant strains, which can release amylase and proteolytic enzymes to convert starch into sugar in the saccharification of cereal vinegar. Moreover, the fruit materials contain more sugar but less starch, so fruit vinegar fermentation does not need molds to convert starch into sugar. This example also shows that appropriate fermentation strains are chosen as starter culture and applied to different vinegars based on various raw materials. In another example, the *Lactobacillus* genus is mainly involved in the AF stage of whey vinegar because whey material has a high pH value and sugar composition. Thus, whey materials are not ideal substrates for yeast growth but suitable for the *Lactobacillus* genus. In the early AF stage of whey vinegar, the pH decreases and whey is converted into lactic acid mainly because of the *Lactobacillus* genus. In later stages of AF, the pH decreases to 5, which is suitable for yeast growth and metabolism. An important example is shown in Tables 1 and 2, in which the microorganisms involved in amber rice vinegar (Komesu) are very different from those in black rice vinegar (Kurosu). Although both of them are rice vinegars that are produced by the same process and the same fermentation method, Komesu is produced from polished amber rice, whereas Kurosu is produced from unpolished black rice (Nanda et al. 2001). Given that the raw material of Komesu is only polished amber rice, many microorganisms disappear during the refining process of rice. Thus, more kinds of strains work in Kurosu than in Komesu because Kurosu's raw material is different from Komesu's raw material. The microorganisms isolated in Kurosu's AF stage are *Lactobacillus lactis*, *Pediococcus acidilactici*, *Aspergillus awamori*, and *Aspergillus usami*, but they are not isolated in Komesu's AF stage (Table 1). In the AAF stage, *Gluconacetobacter xylinus*, *Gluconacetobacter europaeus*, *Gluconacetobacter liquefaciens*, *Gluconobacter oxydans*, and *Lactobacillus acetotolerance* are also involved in Kurosu fermentation (Table 2). In addition, different kinds of strains possess their unique ability to tolerate the sugar concentrations and osmotic pressure, so disparate sugar contents in raw material can also affect the microbial diversity. All of the above findings indicated that raw material has an inseparable relationship with microbial diversity in vinegar fermentation.

The relationship between microbial diversity and starter culture

A number of technological innovations have appeared in the production of a range of dissimilar types of vinegar, among which the most important one is the development of starter cultures to control and accelerate the vinegar's fermentation process (Sokollek and Hammes 1997; Vegas et al. 2013). In contrast to spontaneous fermentation processes, the application of starter cultures will become attractive to vinegar production only in terms of benefits, such as reduced fermentation times, reduced costs, reduced risk of spoilage, improved safety attributes, improved sensory quality, improved process control, and reduced preparation procedures for the final product (Holzapfel 2002). Comprehensive understanding of the culturable fermenting microorganisms is a prerequisite for selecting strains for starter culture implementation (Wu et al. 2012a). For example, the use of *Tetragenococcus halophilus*

as a starter culture during fermentation needs a wide range of salt stresses to promote its metabolism, and this organism plays a crucial role in improving the flavor of soy sauce (Liu et al. 2015). To develop AAB starter cultures, selection criteria should consider AAB metabolic activities, composition of raw material, food safety requirements, applied technology, quality expectations, and desired characteristics of the final product (Gullo and Giudici 2008; Holzapfel 2002).

A starter culture is defined as a preparation or material containing large numbers of variable microorganisms, which will be added to the fermentation of raw materials and produce a fermented food by steering, accelerating, and completing its fermentation process (Holzapfel 2002; Leroy and De Vuyst 2004). The microorganisms that come from starter cultures are the best strains to adapt to raw materials, and they eventually dominate the vinegar fermentation process. Therefore, according to the various kinds of raw materials in vinegar production, starter cultures need to be composed of diverse best-adapted strains. The strains used as starter cultures in industrial applications always include LAB, AAB, molds, and yeasts, and incorporation of these organisms into starter cultures can enhance the nutritional value of vinegar (Ndoye et al. 2009). The distinctive contributions of different strain types to vinegar production have been summarized. LAB populations cause rapid acidification of the raw materials through the production of organic acids, mainly lactic acid, and improve the taste of vinegar (Leroy and De Vuyst 2004). AAB populations mainly contribute in oxidizing ethanol to acetic acid in AAF of vinegar fermentation. The metabolic activities of yeasts and the key enzymes supplied by molds play important roles in AF and saccharification (Wu et al. 2012a). Furthermore, the filamentous fungi *Aspergillus sojae* and *As. oryzae* in starter cultures have been studied extensively. Their production of amylase, proteolytic, and other lytic enzymes has been linked to the transformation of insoluble wheat and soya bean compounds into sugars, free amino acids, water-soluble peptides, and other degradation products that constitute vinegar (Furukawa et al. 2013). Without doubt, different types of starter cultures contain disparate microorganisms. For example, Daqu is the starter culture used in the AF stage, and the dominant beneficial microorganisms in Daqu are molds of the genera *Aspergillus*, *Rhizopus*, and *Mucor*, and yeasts of the genus *Saccharomyces* (Chen et al. 2009; Haruta et al. 2006; Li et al. 2014, 2015). By contrast, the molds of the genera *Aspergillus*, *Monascus*, and *Rhizopus* are the main fungi in koji starter preparation (Kitamoto 2002; Liu et al. 2004). To adapt to a substrate or raw materials, modern starter cultures are always either multiple or single microorganism strains (Holzapfel 2002). Single-strain cultures can improve the accuracy of prediction of metabolic activities and process control and simultaneously increase spontaneous mutation and spoilage through bacteriophage infection and loss of key physicochemical properties (Holzapfel 2002; Ndoye et al. 2009). Mixed-strain cultures are less vulnerable to deterioration, and they are better suited to most small-scale fermentations (De Ory et al. 2002; Sokollek et al. 1998a). In addition, if the starter cultures do not contain sufficient beneficial microorganisms, such conditions may lead to turbidity spoilage of vinegar. Populations and species of yeasts and molds that are not abundant in Daqu samples may lead to turbidity spoilage of vinegar because of the reduction in secretions of protease, glucoamylase, and amylase (Li et al. 2014). Therefore, analysis of the relationship between microbial diversity and starter culture can provide a better understanding of the role of microorganisms in contributing to turbidity spoilage of vinegar. The selection of industrial starter cultures is based on certain basic features, such as adaptation to growth on a specific raw material or substrate, rapid acidification, and phage resistance. For innovations in vinegar production, we should focus on improving the technology of selecting starter cultures (Caplice and Fitzgerald 1999; Giudici et al. 2005; Paul Ross et al. 2002; Sievers et al. 1992).

The relationships among microbial diversity, compounds, and fermentation method

Previously, most manufacturers used spontaneous fermentation, which is a process initiated without the use of a starter inoculum, and it typically results from the competitive activities of various contaminating microorganisms to brew vinegar. To improve fermentation technology, a variety of fermentation methods have been developed in different types of vinegar production. The diverse fermentation methods used can influence the metabolism and growth of microorganisms, as well as enhance their value in the production of potential therapeutic compounds and aroma compounds (Demain 1981, 1999). For instance, thanks to SAV made from several kinds of cereal by spontaneous SSF techniques, the indigenous microorganisms, including 28 LAB isolates, 47 yeast isolates, and 58 AAB isolates, were discovered from its fermentation process. Moreover, SAV produces high contents of organic acids and other compounds because of the fermentation method used.

The contents of organic acids, phenolic composition, and aroma compounds in 36 kinds of vinegars have been summarized. According to several classification methods, multiple fermentation methods that have been used in different types of vinegar fermentation are summarized in Tables 3, 4, and 5. Moreover, the microbial diversity involved in AF and AAF of dissimilar vinegars is summarized in Tables 1 and 2. The summarized data indicated that more types of dominant strain species exist in WRV, black rice vinegar (BRV), ZAV, SAV, kombucha vinegar (KV), PV, WV, ACV, and TBV compared with other vinegars, and these vinegars also have more types of compounds than others. Statistical analysis demonstrated

close relationships among microbial diversity, compounds, and fermentation methods. For example, compared with other rice vinegars, a wide variety of dominant strains have been reported in SAV and ZAV produced by SSF methods, and more compounds are produced by microbial metabolism during fermentation. Moreover, several studies have shown that back-slopping fermentation is a very useful practice because it accelerates the growth of beneficial yeasts and increases the initial number of desirable microorganisms. Although most AAB are very fastidious microorganisms that need special care in the production of true AAB starter cultures, the back-slopping fermentation method is especially advantageous for inoculating AAB cultures. This method not only can inhibit the growth of pathogenic microorganisms, but also reduce spoilage (Millet and Lonvaud Funel 2000). In addition, simply because *Acetobacter pasteurianus* is unable to grow at a high concentration of acetic acid, several vinegars are produced by semicontinuous acetic acid fermentation methods to solve this problem (Fregapane et al. 1999).

In SSF, the solid support systems are applied to provide new methods to manipulate variables that influence the growth and physiology of microorganisms (Barrios González and Mejía 1996). Among vinegar fermentation methods, SSF is an ancient food fermentation method that is widespread in Asian countries to produce C/GV, SAV, and ZAV at a small scale (Table 5). Nowadays, SSF processes have attracted much attention because of their potential not only in the food and pharmaceutical industries, but also in the production of vinegar. However, to date, no large-scale application of SSF has been achieved mainly because of limited microbiological knowledge (Wu et al. 2010). Therefore, the analysis of microbial diversity in vinegar fermentation is also beneficial to improve the fermentation technology.

The relationships among microbial diversity, compounds, and physicochemical properties

Microbial diversity leads to compound and nutrient differences in vinegar fermentation, and it affects the final physicochemical and volatile flavor composition of vinegar (Chen and Xu 2010). In industrial vinegar production, the initial stage of AF often adds enzymes directly to replace the microbial metabolism and speed up the completion of starch saccharification. However, the vinegar produced by this method is obviously not conducive to the formation of flavor substances, because the microorganisms, especially molds, which are used to convert starch to sugars, not only can release many kinds of enzymes, but also can produce secondary metabolites that are endowed with the aroma quality to vinegar. During the fermentation process, yeasts and bacterium metabolize sucrose into a number of organic acids, and the organic acids (especially acetic acid and lactic acid) contributing to vinegar aromas are mainly produced during the AAF stage by metabolic activity of LAB and AAB (Sreeramulu et al. 2000). Numerous compounds are also released in the AF stage, such as fatty acids, succinic acid, and esters, which are mainly produced by the metabolism of yeasts (Charles et al. 2000). Moreover, the type of AF and AAF (inoculated or spontaneous) also influences the number of odor-active compounds. Generally, given that beneficial bacteria are inoculated in vinegar fermentation, the spontaneous process contains a lower percentage of aromatic odor compounds compared with the inoculated process (Ubeda et al. 2012). Meanwhile, certain volatile compounds also have been proven to be useful to characterize the bacterial microbiota involved in the AF and AAF processes (Zhang et al. 2008).

The microorganism metabolites exert great effects on the physicochemical properties of vinegar, decreased pH, and increased acidity because of the accumulation of the acidity secreted by AAB, yeast, LAB, and mold populations (Wu et al. 2012a). Physicochemical properties can also affect microbial diversity involved in vinegar production because the effect of such properties, such as pH and acidity, is responsible for the activity of microorganisms (Cheng et al. 2014a, b). For example, after initiation of AAF, the rapid growth of *A. pasteurianus* immediately increases acidity, which may inhibit the multiplication of other AAB species. The genus *Kloeckera* cannot grow at an environment with an ethanol concentration higher than 4 % (*v*/*v*), whereas more tolerant species, such as the genus *Saccharomyces*, can grow at an environment with up to 14 % (*v*/*v*) ethanol (Rainieri and Zambonelli 2009). During the AF stage, the pH values are suitable for yeast growth and fermentation of sugar into alcohol. In the AAF stage, stressful acidity exerts a fungicidal effect on yeast, so yeasts no longer grow in AAF with increasing acidity; and the pH values during this stage are more suitable for AAB growth and fermentation (Sossou et al. 2009). Thus, yeasts are usually involved in the AF stage, whereas AAB show active participation in the AAF stage. Table 4 shows that the acidity in WRV is 3.5–5.0, the pH is 1.71–3.5, and the residual ethanol is 0.68. By contrast, the acidity in WV is 4–6, the pH is 2.8–3.4, and the residual ethanol is 0.6–2. Given that these physicochemical parameters in WRV are significantly different from those in WV, the dominant species involved in their fermentation processes are also different (Tables 1 and 2).

The relationship between raw material and functionality of vinegar

Vinegar is mostly made from fruit, wheat, barley, and/or peas, which are significant sources of crude protein, carbohydrates, amino acids, and crude fat. Considering that the proportion of these raw materials can differ in different types of vinegar, the

chemical composition and physicochemical features, including organic acids, total amino acids, acidity, and pH values, generally exhibit certain variability. The chemical compositions of raw materials play a vital role in the functionality of vinegar. Tomatoes are a rich source of vitamins, bioactive phenolic, and nutrients compounds, including several polyphenols (chlorogenic and caffeic acid), a large amount of carotenoids (b-carotene and lycopene), naringenin, rutin, and a rich source of trace elements, such as copper, selenium, zinc, and manganese. Thanks to a large amount of functional compounds in the raw materials, tomato vinegar as an anti-obesity therapeutic agent can prevent obesity by suppressing lipid accumulation (Choi et al. 2011; Lee et al. 2013). Onion vinegar is a new functional condiment with specific physicochemical properties and particular composition of raw material, such as high content of minerals, amino acids, and organic acids (Cheng et al. 2014a, b; González Sáiz et al. 2008).

Vinegar can bring numerous benefits for people's health, such as increased serum antioxidant capacity, improved endothelial function, decreased native plasma protein oxidation, reduced platelet aggregation, and protection of low-density lipoprotein against oxidation (Chou et al. 2001). These beneficial effects can be mainly attributed to its content of polyphenols, phenolic compounds, and other functional compounds that are rooted in the raw material (Xia et al. 2010). For example, tea vinegar (kombucha) is produced from tea extract, which is rich in amino acids, proteins, volatiles, antioxidant flavonoids, and lipids; it offers cure or control of dandruff, constipation, bone fractures, cough, cold, diarrhea, toothache, and hypothermia (Johnston and Gaas 2006). Moreover, grape is a rich source of flavonoids and other phenolics, so grape vinegar and grape juices have various health-promoting effects based on their high antioxidant capacity (Dávalos et al. 2005; Makris et al. 2006; Pala and Toklucu 2013).

The relationship between compounds and functionality of vinegar

Different contents of compounds in dissimilar types of vinegar can lead to disparate functions in them. Acetic acid, lactic acid, citric acid, and phenolic compounds are considered important compounds that contribute to the aromatic quality of vinegar, and volatile components of vinegar have been used to distinguish between quality and defective or adulterated samples of vinegar (Durán et al. 2010; Lee et al. 2012). Moreover, thanks to special compounds responsible for the functions of vinegar, various types of vinegars can be differentiated by the discrepancy in the contents of compounds (Del Signore 2001).

Studies revealed that several vinegars possess antioxidant activity, and the main classes of natural antioxidant compounds in nature are phenolic acids and flavonoids in free or complexed forms (Keser et al. 2013). Antioxidant activity of vinegar is well established and generally attributed to polyphenols and phenolic compounds, and the antioxidant capacity of vinegar is mainly determined by DPPH free radical assays (Fan et al. 2009). Table 4 shows that ACV has high DPPH and total phenolic index (TPI) values, so it has high antioxidant activity (Budak et al. 2011). The DPPH values of vinegars fermented from inoculated wines are significantly lower than those of vinegars produced from spontaneous fermentation. However, the TPI values of vinegars from inoculated wines are obviously higher than the vinegars from spontaneous fermentation (Ubeda et al. 2011b). The results indicated that TPI is not the only measure of antioxidant activity, and many antioxidant compounds contribute to the final antioxidant activity of vinegar. The antioxidant activity of vinegar has a positive correlation with the contents of flavonoids, polyphenols, and other compounds. For example, given that the raw material of honey vinegar is fermented and the contents of flavonoid and polyphenol in vinegar decrease significantly, the antioxidant activity of honey vinegar decreases obviously (Dezmirean et al. 2012; Küçük et al. 2007).

In addition to antioxidant activity, polyphenols also benefit endothelin synthesis and oxidation of low-density lipoprotein cholesterols, promote nitric oxide production, and decrease platelet aggregation. For instance, red wine vinegar is demonstrated to lower the blood pressure of humans, because polyphenols in it play an important role in vasodilator actions (Honsho et al. 2005; Takahara et al. 2005). Furthermore, acetic acid is known to inhibit and destroy a number of Gram-negative and Gram-positive microorganisms, and high concentrations of acetic acid are conducive to antimicrobial activity of vinegar. Similar to kombucha vinegar, which exhibits antimicrobial activity, acetic acid is mainly attributable to antimicrobial compounds (Greenwalt et al. 2000; Sreeramulu et al. 2000; Yang et al. 2010).

The compounds of vinegar also play an important role in other special functions of vinegar. First, some studies revealed that volatile enrichment markedly reduces spoilage by reducing fungal spore germination/production (Tzortzakis 2010). Second, sugarcane vinegar contains antimutagenic components, which are estimated to be phenolic, so it may be an excellent acid seasoning with higher levels of physiological function (Yoshimoto et al. 2006). Third, sherry vinegar is a highly appreciated product because of its organoleptic properties, and the organoleptic properties are acquired from the high contents of aromatic and phenolic compounds (García Moreno and Barroso 2002; Parrilla et al. 1999; Tesfaye et al. 2002a). Finally, persimmon vinegar is considered to be a useful intervention for obesity. In persimmon vinegars, acetic acid, citric acid, and lactic acid are the organic acids present in the largest proportion, and they can hinder glycolysis, promote appetite, and enhance the use of fatty acids (Moon et al. 2010). The aforementioned facts clearly indicated that the compounds and functionality of vinegar have a close relationship.

Conclusion

We summarized the dominant microorganism isolated in dissimilar vinegars, as well as various physicochemical properties and crucial compounds in disparate types of vinegar. Moreover, a scientific understanding of the relationships between microbial diversity and other determinant factors in vinegar production was preliminarily elaborated in this review. A summary of microbial diversity, physiological properties, and compounds in vinegar fermentation process will be very useful for future technological developments in vinegar fermentation.

However, based on the summarized data, research on the physicochemical properties and flavor compounds in fruits and cereals vinegars are limited (Tables 3 and 4), so more studies are necessary. To facilitate technological progress in fermentation; address the problem of limited microbiological knowledge about the physiology, ecology, and genetic variability among strains; reduce the variability in fermentation outcomes qualitatively; and improve the control of vinegar quality, quantitative knowledge of the microbial diversity of vinegar is a prerequisite. In addition, more efforts are needed to summarize and analyze the role of microbial diversity in vinegar production, and further research is required to establish microbial ecology and enhance the kinetics of the microbiota in diverse types of vinegar.

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