Chapter 9 Wine and Grape Vinegars

Sylvia Sellmer-Wilsberg

9.1 Wine and Grape Vinegars

9.1.1 Definition and Description

According to the legal definition of the European Union, vinegar is the product obtained from alcoholic and subsequent acetous fermentation of liquids or other substances of agricultural origin (ethanol, wine, cider, perry, or liquors obtained from cereals, including malted barley). In the USA, this definition is extended to include synthetically produced alcohol used for acetous fermentation.

Some kinds of vinegar are: spirit vinegar, wine vinegar, fruit vinegar, cider vinegar, grain vinegar and malt vinegar. Mashes obtained by the alcoholic fermentation of natural sugar containing liquids also serve as raw material. The vinegar is designated according to the particular raw material used. For instance, wine vinegar is produced by acetic acid fermentation of grape wine, cider vinegar is produced from fermented apple juice, etc.

Regional speciality vinegars such as traditional balsamic vinegar from Modena (Italy) and sherry vinegar from Jerez (Spain) are described in the following chapters.

Wine vinegar is made from red or white wine, and is the most commonly used vinegar in the households of the Mediterranean countries and Central Europe. As with wine, there is a considerable range in quality. Better-quality wine vinegars are matured in wood for up to 2 years and exhibit a complex flavour. The most expensive wine vinegars are made from individual varieties of wine, such as Champagne, Sherry or Pinot Grigio.

9.1.2 Composition

As well as acetic acid and ethanol, vinegar contains secondary constituents which play an important role with regard to its smell, taste and preservative qualities. These constituents have their origin in the raw material, in the added nutrients, and in the water used for dilution. They are also formed by acetic acid bacteria, or they are a product of the interaction of the different components.

Wine vinegars contain the same spectrum of amino acids as spirit vinegar, but in larger amounts. Galoppini and Rotini (1956) and Rotini and Galoppini (1957) found that during acetous fermentation, acetylmethylcarbinol develops in varying quantities. In an ether-pentane extract of wine vinegar, Kahn et al. (1972) identified 42 compounds. Besides the substances which had been found in spirit vinegar, compounds derived from higher alcohols, such as isopentyl acetate, isovalerylalde-hyde, or β -phenethyl acetate are of particular interest. Garcia et al. (1973) analysed 20 types of wine vinegar. Most of them contained acetoin and butylene glycol, but only seven contained diacetyl.

Polyphenolic compounds have been shown to be of great interest with regard to the stability of wine vinegars. Galvez et al. (1994) identified polyphenolic compounds by using HPLC separation. They stated that, as a rule, vinegars obtained from wines exhibit a greater number and content of polyphenolic compounds than vinegars obtained from apples or honey. Those originating from Rioja wines showed the maximum number, followed by those derived from sherries. In wine vinegars the following substances were identified: gallic acid, p-OH-benzaldehyde, caffeic acid, vanillic acid, syringic acid, p-coumaric acid, anisaldehyde, epicatechin, sinapic acid and salicylaldehyde. The phenolic compounds are generally contributed by the solid parts of the grapes. Therefore, in the case of wines kept in longer contact with the grapes (as in the case with Rioja wines), a larger amount of polyphenols will be extracted.

9.2 Technology

9.2.1 Fermentation

Nowadays, wine vinegars are mostly produced in the same way as spirit (alcohol) vinegar using the semi-continuous submerged process. Stainless steel fermenters (Figure 9.1) of a size between 1000 and 110,000 L working volume equipped with a self-aspirating aeration system (Figure 9.2), ensuring a short and highly efficient mixing of alcohol, water and nutrients, are used most frequently. Usually wine vinegar is produced in smaller fermenters (20-40 m³) than those used for the production of alcohol vinegar.

In the semi-continuous process, wine vinegar with an acetic acid concentration of 8-14% is produced (see Figure 9.3). Each fermentation cycle takes about the same time as the preceding and following cycles. The starting concentration of each cycle is 7-10% acetic acid and about 5% ethanol. When an alcohol concentration between 0.05% and 0.3% has been reached in the fermentation liquid, a quantity of vinegar is discharged from the fermenter. Refilling with new mash of 0-2% acetic acid and 12-15% alcohol leads to the starting concentrations for the



Figure 9.1 Example of a submerged vinegar fermenter with an annual production capacity of 18 million L of vinegar containing 10% acetic acid



Figure 9.2 Highly efficient aeration system in a fermenter for wine vinegar production

new cycle mentioned earlier. Discharging must be carried out quickly to avoid complete alcohol depletion. Charging must be done slowly under constant fermentation temperature and rapid mixing. The duration of a cycle is between 18 and 30 hours, depending on the total concentration and the efficiency of the aeration system.

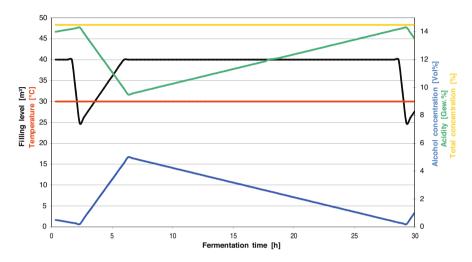


Figure 9.3 Ethanol, acidity, volume, temperature and total concentration profiles in a semibatch process for wine vinegar production (courtesy of Cetotec Biotechnologie GmbH)

Continuous fermentation is only possible up to a maximum of 9-10% acetic acid, because the specific growth rate of the bacteria decreases with decreasing ethanol concentration. To obtain high yields, the fermentation must be carried out at low alcohol concentrations.

Some vinegar manufacturers in Italy and Spain uses a special two-stage process, where two fermenters are combined. In the first step, the alcohol is degraded to 2-3%, then a certain quantity of vinegar is transferred into a second fermenter. The first fermenter is then resupplied with new mash. In the second fermenter, the fermentation continues until the alcohol is almost depleted. The whole quantity of finished vinegar is then discharged.

9.2.1.1 Nutrients

Most natural raw materials do not require the addition of extra nutrients. Some grape wines require the addition of ammonium phosphate for an optimal fermentation. Ready-to-use nutrients are commercially available, containing a complex mixture of ammonium and potassium salts, vitamins and trace elements. Essentially, nutrients should be added sparingly in order to exert a selection pressure which leads to a low requirement for nutrients (Ebner et al., 1996b).

9.2.2 Storage

During the production process of wine and fruit vinegar, storage is an important factor. During storage, the quality of the vinegar improves considerably, and organic extracts and bacteria precipitate, thus helping further processing.

In the course of acetous fermentation, the pH value of the fermenting mash decreases. Vinegars obtained from natural raw materials therefore show some instability with respect to the solubility of previously dissolved substances. The less the pH changes during fermentation, the longer this lability lasts. A freshly produced cider vinegar, for example, may need several months to become stable. Alcohol vinegar does not show this instability. Vinegar for storage should preferably be undiluted, i.e. it should be the same as when it was discharged from the fermenter. In storage the quality of vinegar always improves, regardless of the type of vinegar or the sort of wine it was made from. The ageing of wine vinegar involves many complicated reactions, as described in detail by Mecca et al. (1979). Vinegar must have a pure aroma which imparts the flavour of the raw material.

9.2.3 Filtration

The filtration step following the storage is essential in order to produce a microbiologically stable product. Traditional methods of vinegar clarification by fining and pre-coat filtration are still in use, especially for the treatment of different kinds of wine vinegar. However, newer micro- and ultrafiltration methods are gaining in popularity, especially in the large European and American factories.

9.2.3.1 Traditional Methods

Filters with a diatomaceous earth coating are well suited to most vinegars, whether aged or non-aged, fined or unfined. A filter layer of approximately 1 mm thickness of diatomaceous earth or cellulose is placed on a coat of acid-resistant steel, wood or nylon. The quality of this filter coat determines the flow rate of vinegar filtered through the layer, and the brilliance of the product. During filtration, diatomaceous earth is added continuously to keep the growing filter cake as permeable as possible. As soon as the filtration pressure has increased and the filter capacity has decreased too much, filtration has to be stopped and the filter has to be cleaned and prepared for a new filtration. The main disadvantages of traditional, labour-intensive filtration techniques are the time-consuming method and the disposal of the filter aids. Complete, largely automatic filters with both horizontal and vertical filtering surfaces are now available on the market.

9.2.3.2 Continuous Microfiltration

Cross-flow filtration of vinegar using microporous hollow fibre membranes is nowadays becoming more and more important (Figure 9.4). The raw vinegar is



Figure 9.4 Model of a cross-flow filtration plant used for continuous microfiltration of vinegar

conducted at high speed diagonally towards the membrane surface, thus preventing the spontaneous formation of a coating. The constant flow ensures a clean surface, which is essential for a high, stable filtration performance. In most cases the microfiltration modules used in vinegar production are equipped with capillary membranes with a pore size of 0.2 μ m (Sellmer-Wilsberg and Rodemann, 1998).

Vinegar is a cheap substance; filter costs must therefore be kept low. Consequently the repeated and long-term use of the filter modules is important. The unavoidable formation of a film on the membrane, reducing the filtration rate, must be prevented for as long as possible. Easy, repeated and mainly automatic cleaning of the membrane is also important. Modern cross-flow filters with polysulphone or ceramic membranes are often used for the filtration of various kinds of vinegar.

9.3 Microbiology

The ecology and biology of the acetic acid bacteria are relatively well known due to the considerable economic profits and losses that these bacteria cause in industry. Since the first description of acetic acid bacteria, an extensive literature has been accumulated.

The older literature focused on the acetic acid bacteria used in vinegar manufacture and their role as spoilers in beers and wines. The occurrence of acetic acid bacteria in other niches, such as flowers, fruits, beehives, 'tea fungus' and palm wine was not described until much later. In the past 20 years, very many publications from research groups in Japan have appeared, dealing with bacteria from submerged fermentations, immobilized bacteria, and especially with genetic engineering of acetic acid bacteria.

The assignment of the acetic acid bacteria to the genera *Acetobacter*, *Gluconacetobacter* or *Gluconobacter* generally poses little difficulty. The identification at the species level, however, is sometimes more problematic.

9.3.1 Summary and Classification

The microorganisms which oxidize ethanol to acetic acid are commonly called acetic acid bacteria. This special primary microbial metabolism at low pH of the surrounding medium differentiates them from all other bacteria. Acetic acid bacteria are polymorphous.

Cells are Gram-negative, ellipsoidal to rod-shaped, straight or slightly curved, 0.6-0.8 μ m by 1.0-4.2 μ m, occurring singly, in pairs, or in chains. There are non-motile forms and motile forms with polar or peritrichous flagella. They are obligately aerobic; some produce pigments, some produce cellulose.

Attempts to classify acetic acid bacteria have been summarized by Ebner et al. (1996c). At that time, a major contribution to their taxonomy was made by DNA-rRNA hybridization studies (Gillis and De Ley, 1980). A first conclusion from this work was that *Gluconobacter* and *Acetobacter* were closely related groups, justifying their union in the family *Acetobacteraceae*, clearly distinguishable as a separate branch in Superfamily IV, containing *Rhodopseudomonas*, *Beijerinckia*, *Agrobacterium*, *Rhizobium*, etc.

Before the last edition of *Bergey's Manual*, a set of 32 features was given to differentiate the genera *Gluconobacter*, *Acetobacter* and *Frateuria*; however, not all of these features are necessary for a satisfactory identification (De Ley et al., 1984). The ability to over-oxidize acetate identified the strains from 'high-acid' fermentations as members of the genus *Acetobacter*, and thus separates them from the genera *Gluconobacter* and *Frateuria*. Swings (1992) divided *Acetobacter* into seven species: *A. aceti*, *A. liquefaciens*, *A. pasteurianus*, *A. hansenii*, *A. xylinum*, *A. methanolicus* and *A. diazotrophicus*. In 1997, Yamada et al. proposed a new genus, *Gluconacetobacter* (previously recognized as a subgenus within *Acetobacter*), where several 'old' vinegar-producing *Acetobacter* species are now ascribed, such as *Gluconacetobacter europaeus* and *Gluconacetobacter xylinus*. The present assessment of acetic acid bacteria taxonomy is reported in the second edition of *Bergey's Manual of Systematic Bacteriology* (Sievers and Swings, 2005), as described in Chapter 3.

9.3.2 Required Properties of Industrially Used Strains

If one considers the interest that acetic acid bacteria have aroused in many microbiologists, it is astonishing how little effect the available information about these bacteria has had on vinegar manufacture. This is particularly striking in regard to use of the pure culture approach in the vinegar industry. Henneberg (1926) pointed out the enormous advantages of introducing pure cultures in vinegar manufacture: it would reduce the occurrence of vinegar eels, 'Kahm' yeasts, and the unwanted contaminant *A. xylinus* (now *Ga. xylinus*). It would also permit the selection of suitable strains possessing the required technological and commercial qualities. Shimwell (1954) isolated an *A. aceti* strain as a true 'working' strain. With this strain he produced up to 12% malt, spirit or wine vinegar of excellent quality at rates as fast as in the normal production process. Another strain, thought to be the 'active one' in a quick vinegar process, was isolated from beechwood shavings by Wiame et al. (1959). However the original strain was lost (Suomalainen, 1962), which demonstrates the difficulties in isolating and growing *Acetobacter* strains from industrial vinegar fermentations on solid media.

Considerable success was achieved by propagating bacteria from generators in Japan on a special double-layer agar. The bacteria isolated on this medium have been described as '*Acetobacter polyoxogenes*' (Entani et al., 1985). However, the species *A. polyoxogenes* has not been validly published, and the strain is not available from the Japan Collection of Microorganisms, due to problems of propagation and preservation.

A new species in the genus Acetobacter, for which Sievers et al. (1992) proposed the name Acetobacter europaeus (now Ga. europaeus), has been isolated and characterized in pure culture from industrial vinegar fermentations in Germany and Switzerland. All investigated strains isolated from submerged fermenters and trickle generators had very low (0-22%) DNA-DNA similarities with the traditional type strains of the genera Acetobacter and Gluconobacter. Phenotypical differentiation at the species level of the genus Acetobacter is rather difficult, since different strains of a single species do not necessarily utilize the same carbon source. A useful and significant criterion for the identification of Acetobacter europaeus (now Ga. europaeus) is its strong tolerance to acetic acid at a concentration of 4-8% in AE-agar, and the absolute requirement of acetic acid for growth.

Sokollek et al. (1998) isolated two *Acetobacter* strains from red wine and cider vinegar fermentations and described them as new species: *Acetobacter oboediens* sp. nov. and *Acetobacter pomorum* sp. nov. Comparative analysis of the 16S rRNA sequences revealed >99% similarity between the isolated strain LTH 2460 and the type strains of the related species *A. europaeus* (now *Ga. europaeus*) and

A. xylinus (now Ga. xylinus), and also between strain LTH 2458 and Acetobacter pasteurianus. On the other hand, low levels of DNA relatedness (<34%) were determined in DNA-DNA similarity studies. This relatedness below the species level was consistent with specific physiological characteristics, permitting clear identification of these strains within established species of acetic acid bacteria. Based on these results, the species Acetobacter oboediens sp. nov. and Acetobacter pomorum sp. nov. were proposed, but were then transferred within the genus Gluconacetobacter as Gluconacetobacter oboediens and Gluconacetobacter pomorum (Sievers and Swings, 2005).

Independent of all these problems and difficulties, the vinegar industry's first and foremost interest is to use a strain of acetic acid bacteria which tolerates high concentrations of acetic acid, which requires small amounts of nutrients, which does not over-oxidize the acetic acid formed, and which yields high production rates.

The vinegar industry has always worked with acetic acid bacteria which, in most cases, are not derived from pure cultures. The astonishing fact that common microorganisms used on a large scale for industrial vinegar production have not been properly described and characterized in taxonomic terms can be explained by the difficulty of cultivation of these bacteria on semi-solid media.

Industrial submerged vinegar fermentations are started by inoculation with 'inoculation vinegar', i.e. microbiologically undefined remains from previous fermentations. The lack of defined pure starter cultures is due to the previously mentioned problems in the isolation of the *Acetobacter* strains responsible for high acid production.

Acetic acid fermentation can be carried on for years without interruption or any decrease in efficiency or yield, as long as suitable reaction conditions are chosen to allow an ongoing selection process that favours only those organisms which tolerate high acidity and can survive on a minimum of nutrients. From industrial practice it has long been known that the properties of a newly isolated strain of acetic acid bacteria may change from the very first moment of cultivation in Petri dishes, and that this strain, if cultivated over a number of generations, may show other properties, especially as far as the adaptation to certain concentrations of acetic acid is concerned, but also regarding its phenotypic features. Therefore, in practice, the transformation of acetic acid bacteria from a surface culture to a submerged culture and *vice versa* is highly problematic with regard to the quantitative and qualitative results as long as total concentrations higher than 12% are to be maintained. The mechanism of this extremely high variability, which has not been described so far for other bacteria, is unclear.

9.4 Vinegar and Food Law

A legal assessment of vinegar is of great importance in order to define, within the framework of national and international legislation, whether a product is synthetic acid or biologically obtained vinegar, and whether it is a true wine or fruit vinegar, or a blend.

9.4.1 Differentiation between Vinegar and Acetic Acid

The problem can be approached from two angles.

- The specific impurities in the acetic acid, which go back to its production process, may serve as a criterion for differentiation. A survey of standard processes for synthetic acetic acid is given by Staege (1981). However, as acetic acid is nowadays produced with a high purity, the secure identification of polluting substances has become more difficult.
- A characterization of the specific compounds in fermentation vinegars is therefore growing in significance. A great variety of qualitative reactions and quantitative determinations are described in the literature.

9.4.2 Differentiation between Wine Vinegar and Spirit Vinegar

An accurate and reliable differentiation between true wine vinegars and their blends with spirit vinegar, or more generally between vinegars rich in extract and their blends, is of particular importance.

Generally, a good method is the identification of the specific fruit acids, such as tartaric acid in wine or malic acid in cider vinegar. A formol titration to identify amino acids may also be applied. On the other hand, fruit-specific acids and also amino acids can easily be added. Full analyses are often the best way to decide whether only pure wine has been used, or whether spirit vinegar has been added (Llaguno, 1977). However, and this will generally apply to the methods of differentiation, the limits of confidence for an estimate of the quantity of spirit vinegar added to wine vinegar are rather narrow.

9.4.3 Adulteration of Wines

The problem is how to prove the use of low-quality grape pomace wine, pome wine, spoilt vinegar wine, or even synthetic wine. For all these investigations (see Sections 9.5.1.1 and 9.5.1.2) a newly developed method offers very promising results. The authentication of the origin of vinegars can be determined by a modern isotopic method, called SNIF-NMR (site-specific natural isotopic fractionation-nuclear magnetic resonance spectrometry). This method was originally developed at the University of Nantes (Dumoulin, 1993) in France. Eurofins Laboratoires, a research institute in Nantes, carried out a preliminary research project in order to extend and complete the results of the application of the SNIF-NMR method, which is an official EEC analysis for wines, to the field of vinegars. The first results have demonstrated the applicability of the SNIF-NMR method to detecting added synthetic acid to vinegar and, more generally to determining the botanical origin of vinegar (wine, apple, malt, cane or beet alcohol, etc.). With this method it is possible not only to identify the raw materials of the corresponding vinegar but also to ascertain the origin of the grapes, e.g. from the

northern part of Italy. For this purpose a database of authentic vinegars has been compiled by Eurofins.

The detection threshold for adulterations with synthetic acid to vinegar of known and unknown geographical origin is 5% and 10%, respectively. The detection threshold in the case of alcohol vinegar being added to wine vinegar of known and unknown geographical origin is 10% and 20%, respectively.

The present procedure for authentication of vinegars using 2H-NMR spectroscopy and mass spectroscopy (MS) on acetic acid and water is ready to be made official by including it in the Code of Practice.

9.5 Analysis of Vinegar

Vinegar is analysed for two purposes: for process control by general routine methods, and to gain a comprehensive knowledge of its chemical constituents.

9.5.1 Detection of Alcohol Vinegar in Wine Vinegar

A safe differentiation between true wine vinegars and their blends with spirit vinegar, or generally between vinegars rich in extract and their blends, is of particular importance. Generally, a good method is the identification of the specific fruit acids, such as tartaric acid in wine or malic acid in cider vinegar. A formol titration to identify amino acids may also be applied. On the other hand, it is very easy to add fruit-specific acids and amino acids to any vinegar.

9.5.1.1 Traditional Methods

The following methods have been in use for the differentiation of alcohol from spirit vinegar (for complete details, see Ebner et al., 1996a):

- ratio of acidity to dry residue
- UV-absorption
- chromatography
- determination of potassium.

All these methods are not very specific or, as mentioned above, can be manipulated easily.

9.5.1.2 SNIF-NMR Method

For the detection of alcohol vinegar in wine vinegar, the SNIF-NMR-method is the most specific and precise method (see Section 9.4.3).

The detection threshold of adulteration with alcohol vinegar is:

- 10% of alcohol vinegar into wine vinegar of known geographical origin
- 20% of alcohol vinegar into wine vinegar of unknown geographical origin.

References

- De Ley J, Gillis M, Swings J (1984) Family VI Acetobacteraceae. In: Krieg NR, Holt JG (eds) Bergey's Manual of Systematic Bacteriology. Williams and Wilkins, Baltimore, MD, Vol 1, pp. 267–277
- Dumoulin M (1993) SNIF-NMR: A New Analysis to Characterize the Plant Origin of Vinegar. Eurofins Laboratoires, Nantes, France
- Ebner H, Follmann H, Sellmer S (1996a) Vinegar. In: Rehm HJ, Reed G (eds) Biotechnology, 2nd edn. VCH Weinheim, Vol 9:581–591
- Ebner H, Sellmer S, Follmann H (1996b) Acetic acid. In: Rehm HJ, Reed G (eds) Biotechnology, 2nd edn. VCH Weinheim, Vol 6:381–401
- Ebner H, Follmann H, Sellmer S (1996c) Vinegar. In: Ullmann's Encyclopedia of Industrial Chemistry, Vol A27. VCH Weinheim, pp. 403–418
- Entani E, Ohmori S, Masai H, Suzuki KI (1985) Acetobacter polyoxogenes sp. nov., a new species of an acetic acid bacterium useful for producing vinegar with high acidity. J Gen Appl Microbiol 31:475–490
- Galoppini C, Rotini OT (1956) Ulteriori indagini sulla formazione dell'acetilmetilcarbinolo nella fermentazione acetica. Ann Fac Agrar Univ Pisa 17:99–111
- Galvez MC, Barroso G, Perez-Bustamante JA (1994) Analysis of polyphenolic compounds of different vinegar samples. Z Lebensm Unters Forsch 199:29–31
- Garcia OR, Casaballido-Estevez A, Castana-Torres M (1973) Vinegars. II. Content of diacetyl, acetoin, butylene glycol and alcohol. Ann Brom 25:121–145
- Gillis M, De Ley J (1980) Intra- and intergeneric similarities of the ribosomal ribonucleic acid cistrons of Acetobacter and Gluconobacter. Int J Syst Bacteriol 30:7–27
- Henneberg W (1926) Handbuch der Gärungsbakteriologie, Bd I, 2. Aufl, Berlin
- Kahn HJ, Nickol GB, Conner HA (1972) Identification of volatile compounds in vinegars by gas chromatography-mass spectrometry. J Agric Food Chem 20:214–218
- Llaguno C (1977) Quality of Spanish wine vinegars. Process Biochem 12:17-46
- Mecca F, Andreotti R, Verdonelli L (1979) L'Aceto. Edizioni AEB, S. Polo, Brescia, Italy
- Rotini OT, Galoppini C (1957) L'Acetilmetilcarbinolo, la fermentazione acetica e la genuinità degli aceti del commercio. Ann Sper Agrar 11:1355–1372
- Sellmer-Wilsberg S, Rodemann K (1998) Einsatz mikroporöser Hochleistungsmembranen in der Essigfiltration. GIT Lab Fachz 42:881–883
- Shimwell JL (1954) Pure culture vinegar production. J Inst Brew 60:136-141
- Sievers M, Swings J (2005) Family II Acetobacteriaceae Gills and DeLoy 1980. In: Garrity GM, Winters M, Searles DB (eds) Bergey's Manual of Systematic Bacteriology, 2nd edn. Springer, New York, Vol 2:41–48
- Sievers M, Sellmer S, Teuber M (1992) Acetobacter europaeus sp. nov., a main component of industrial vinegar fermenters in central Europe. Syst Appl Microbiol 15:386–392
- Sokollek J, Hertel C, Hammes W (1998) Description of Acetobacter oboediens sp. nov. and Acetobacter pomorum sp. nov., two new species isolated from industrial vinegar fermentations. Int J Syst Bacteriol 48:935–940
- Staege H (1981) Essigsäure aus Kohle unter Anwendung der Flugstromvergasung nach Koppers-Totzek. Verfahrenstechnik 15
- Suomalainen H (1962) Acetobacter rancens: Reinkultur beim Schnellessigverfahren. Brauwissenschaft 15:356–357
- Swings J (1992) The genera Acetobacter and Gluconobacter. In: Balows A, Trüper HG, Dworkin M, Harder W, Schleifer KH (eds) The Prokaryotes, 2nd edn. Springer, New York, Vol 3: 2268–2286
- Wiame JM, Harpigny R, Dothey RG (1959) A new type of Acetobacter: Acetobacter acidophilum prov. sp. J Gen Microbiol 20:165–172
- Yamada Y, Hoshino K, Ishikawa T (1997) The phylogeny of acetic acid bacteria based on the partial sequences of 16S ribosomal RNA: the elevation of the subgenus Gluconoacetobacter to the generic level. Biosci Biotechnol Biochem 61:1244–1251