Saudi Journal of Biological Sciences 29 (2022) 1565–1576

Contents lists available at ScienceDirect

Saudi Journal of Biological Sciences

journal homepage: www.sciencedirect.com

Review

Recent trends in microbial flavour Compounds: A review on Chemistry, synthesis mechanism and their application in food

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ARTICLE INFO

Article history:
Received 1 September 2021
Revised 17 October 2021
Accepted 4 November 2021
Available online 12 November 2021

Keywords:
Aroma compounds
Biotransformation
Microbiota
Acetaldehyde
Flavour characteristics

ABSTRACT

Aroma and flavour represent the key components of food that improves the organoleptic characteristics of food and enhances the acceptability of food to consumers. Commercial manufacturing of aromatic and flavouring compounds is from the industry's microbial source, but since time immemorial, its concept has been behind human practices. The interest in microbial flavour compounds has developed in the past several decades because of its sustainable way to supply natural additives for the food processing sector. There are also numerous health benefits from microbial bioprocess products, ranging from antibiotics to fermented functional foods. This review discusses recent developments and advancements in many microbial aromatic and flavouring compounds, their biosynthesis and production by diverse types of microorganisms, their use in the food industry, and a brief overview of their health benefits for customers.

Contents

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Peer review under responsibility of King Saud University.

Production and hosting by Elsevier

https://doi.org/10.1016/j.sjbs.2021.11.010

1. Introduction

Flavours and aromas play a major role in our everyday lives. They are available in food and cosmetics. Nowadays, demand for natural ingredients rather than a chemical is increasing and it is the same for flavour compounds also (Roman et al., 2017). Flavouring compounds in the food, perfumes, and pharmaceutical industries are widely used. In general, plant compounds are the main sources of natural flavour though some of them are also synthesized chemically. Culturing plant cells is a promising process for flavour and aroma production. This method is based on the biochemical, genetic, and totipotential capabilities of plant cells (Ayseli and Ayseli, 2016; Zakaria and Kamal, 2016).

On the other side, biotechnology advances make it possible to synthesize natural flavours economically and successfully at a commercial scale. Enzymes are used for biotransformation but entire microorganisms' cells are very promising because the microorganisms can easily be generated and used in the fermenters. The use of biotransformation systems allows biotechnology products to be labeled as natural. Market analysis indicates that customers prefer natural ingredients while artificial ingredients have many side effects like allergy, nausea, chest pain or headache and sometimes even detrimental consequences like cancer, negative effects of neurons, kidney damage, etc. (Roman et al., 2017).

Besides studying the chemical properties of natural volatile flavour compounds (VFCs), which cause aroma and flavours perceived, some studies have shown that their antioxidant, anticancer, anti-inflammatory, and anti-obesity activities may have potential applications to human health (Caron et al., 2021; Paulino et al., 2021). In addition, market demand shows a trend to natural goods, with the bio-generation of trade-relevant natural volatile aroma compounds, especially the synthesis or biological transformation by enzymes or whole cells in traditional aqueous solution, mainly centered within industry and academic sectors (Ayseli and Ayseli, 2016; Caron et al., 2021).

There is a great deal of curiosity about natural products. This drives the fragrance industry to create new methods for extracting compounds with natural aromas. Bioconversion is another form of this natural synthesis. It is well known that the production of volatile aroma compounds by enzymes or microorganisms for the food industry provides various advantages over conventional methods (Paulino et al., 2021). The use of solid-state fermentation in conjunction with submerged fermentation often provides higher yields or superior product features with reduced costs. Furthermore, owing to its high boiling point and high temperature at which it evaporates, water impedes the isolation and purification processes as well as the process integration (Try et al., 2018).

In food production, microbiological contamination can pose a health hazard by inducing diseases such as diarrhea, stomach cramps, vomiting, and even death. The intake of fresh and minimal processed foods has been seen a drastic rise in outbreaks of food-borne conditions in recent decades due to *Enterobacter aerogenes*, *Escherichia coli* O157:H7, *Listeria monocytogenes*, *Pseudomonas aeruginosa*, *Staphylococcus aureus,* and *Salmonella* (Al-fekaiki et al., 2017). The *in vitro* studies report the antimicrobial action of natural VFCs. The natural flavours of phenolic compounds enter the cell membrane and disrupt the lipid structure of the membrane. Theoretical abilities also disrupt the permeability of the membrane and impacts disrupt cellular ion gradients (Tometri et al., 2020).

In view of the above discussion, this study presents the current progress in several VFCs, their microbial synthesis as well as the high potential for commercial use in foods. The current review also assesses the antimicrobial potential of different flavour compounds from the enzymatic and microbial origin in addition to exploring their utilization in milk-based products, meat, and seafood processing. Fig. 1 accurately depicts the overview of this review study.

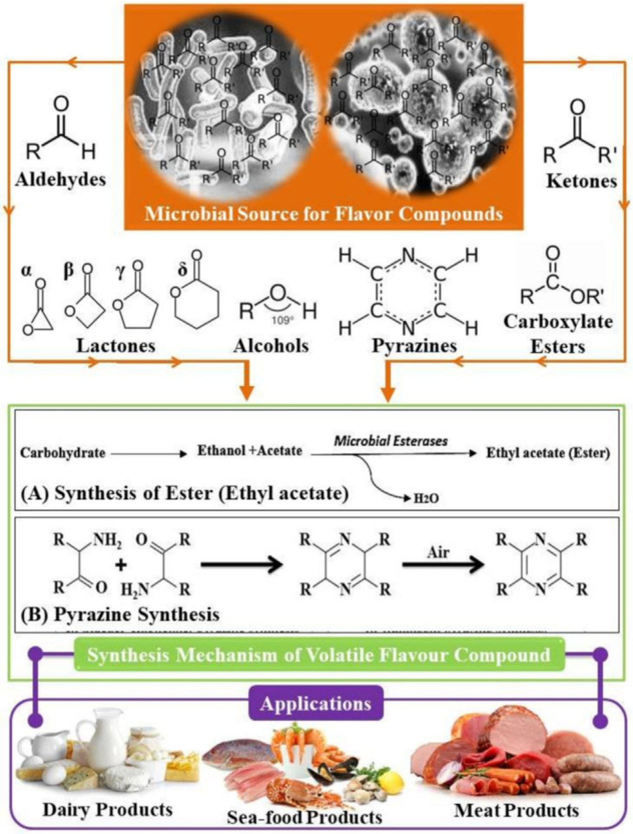


Fig. 1. A graphical summary of this study of recent trends in microbial flavour compounds, chemistry, synthesis mechanism and their application in food.

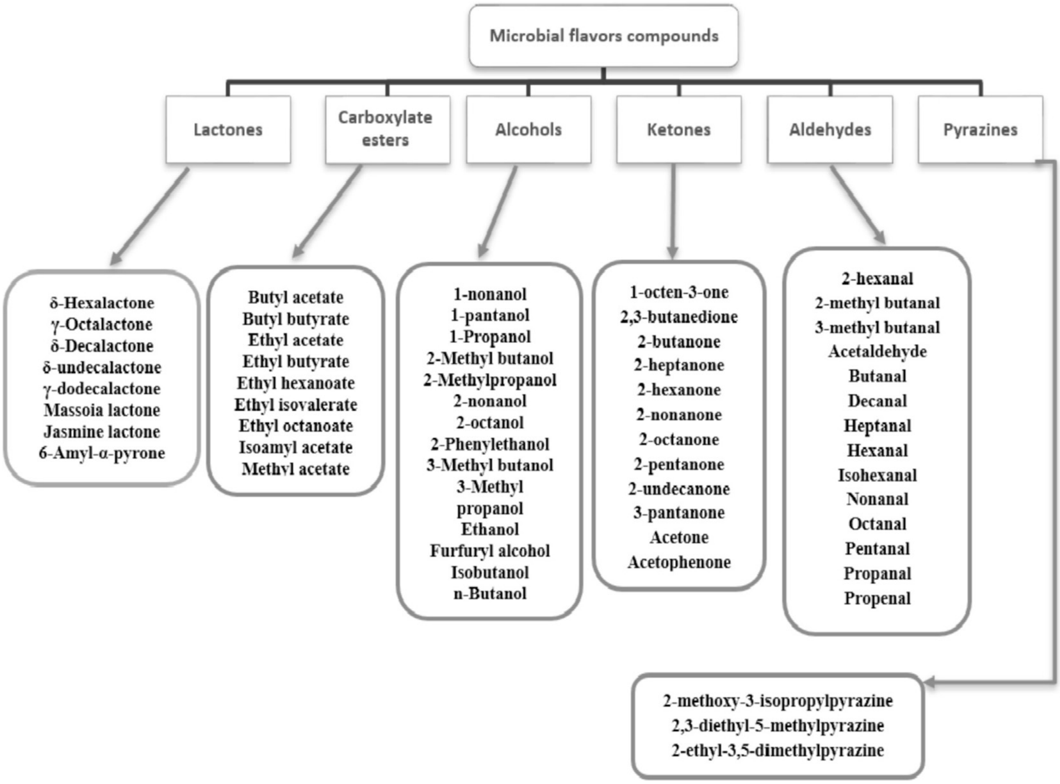


Fig. 2. Classification on the basis of chemical compositions for microbial VFCs.

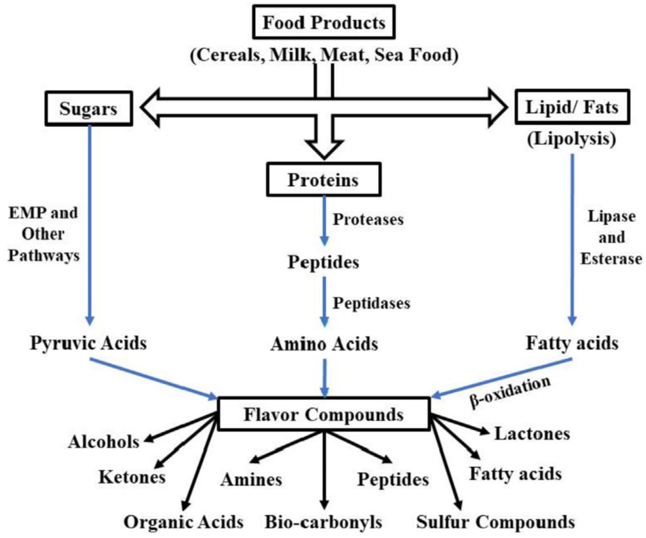


Fig. 3. Biosynthesis of flavours by different microorganism in various food products.

2. Types of microbial flavours compounds

Fig. 2 indicates the grouping of VFCs by chemical composition. Microorganisms have since already been used in many foodstuffs to produce flavours. Microbes are used to preserve, modify, and flavour products such as wine, beer, fermented vegetables and milk, soybeans, pickles, and meat vinegar. Different microorganisms follow the specific metabolic pathway to produce specific flavour compounds as summarized in Fig. 3. As mentioned above, microbial strains can either be used to produce VFCs *in-situ* or in suitable substrates from which VFCs are obtained and then used in various foodstuffs (Dan et al., 2019; Wang et al., 2020a, b; Zinjanab et al., 2021). In Table 1**,** the outcomes of various researchers for the biosynthesis of VFCs from different substrates by specific microbial species are compiled. The following sections discuss the most relevant category of VFCs used in the food industry and their microbial production:

2.1. Lactones

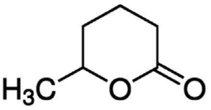
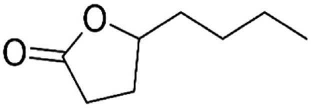
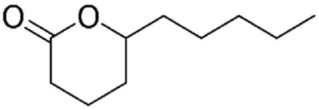
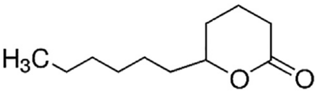
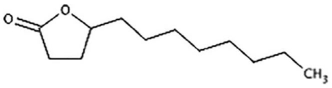
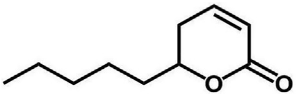
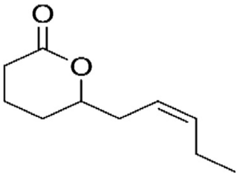
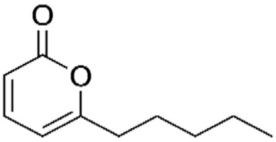
Lactones are internally formed cyclic esters of γ- and δ-hydroxy acids which are in combination with their corresponding alcohols. These lactones have a wide flavour composition that contributes primarily to too many flavours in dairy products, including buttery, coconut, creamy, fruity, nutty, or sweet flavours. Free lactones and their precursors come from fresh butter with a sweet fruity fragrance. In animal fats as well as auto-oxidized vegetable oils, δ-lactones are also found. This gives candies and pastries a strong flavour whereas, the weak flavour of tea, strawberry, raspberry, coconut, and butter is due to the presence of 5-methylpentanolide or δ-Hexalactone (Bhari and Singh, 2019; Kendirci et al., 2020). Table 2 discusses some of the other major VFCs of the lactones group with their chemical structure and food sources.

δ-Decalactone is a key lactone for the flavouring industry also called decan-4-olide and is used as a dairy and fruit flavour. It has an incredibly strong smell and a creamy taste with a concentration of<5 parts per million (ppm). Peach fruit is the best source of this VFC which can be used as the aroma of apricot (*Prunus armeniaca*), peach (*Prunus persica*), coconut (*Cocos nucifera*), date (*Phoenix dactylifera*), maple (*Acer* spp.), pear (*Pyrus* spp.) and butterscotch. This VFC can be commercially synthesized in a biochemical reaction that is catalyzed by *Candida guillermondii* lipase or *Yarrowia lipolytica* by the transformation of the ricinoleic acid found in the oil of the castor plant (*Ricinus communis*). δ-

Table 1
Biosynthesis of flavours from different substrates by microorganisms.

List of TablesCompound	Microorganisms Involved	Substrate	References
δ-Decalactone	*Aspergillus niger*, *Cladosporium suaveolens* and *Pichia etchelisii*	Oil of *R. communis*	Prabakaran et al. (2020)
	Monilia fructicola, *Rhodotorula glutinis* and *Sporobolomyces odorus*	Castor oil	Bhari & Singh (2019)
	Yeast species	11-hydroxy palmitic in sweet potatoes (*Ipomoea batatas*)	Vandamme & Soetaert (2002)
Octalactones	*Mortinella* spp.	Octanoic acid (caprylic acid) found in coconut oil	Vandamme & Soetaert (2002)
Ethylacetate	Yeasts including *Cyberlindnera jadinii*, *Kluyveromyces marxianus*, and *Wickerhamomyces anomalus*	Sugars or ethanol	Fan et al. (2019); Zhang et al. (2020b)
2-phenylethanol	*Saccharomyces cerevisiae*	Fermented wine	Liang et al. (2020)
2-phenylethanin	*Hansenula anomala*, *K. marxianus*, and *S. cerevisiae*	2-phenylalanine	Chantasuban (2016)
Diacetyl	LAB such as *Leuconostoc* sp., *Lc. lactis* subsp.*lactis* serover *diacetylactis*and Yeasts	Milk, Synthetic media	Rosca et al. (2016); Wang et al. (2019b)
Acetaldehyde	Lactobacilli and Yeasts	Milk, Synthetic media	Dan et al. (2019); Rosca et al. (2016)
Benzaldehyde	*Pseudomonas taiwanensis* (engineered)	Supplimented medium of glucose or glycerol	Otto et al. (2020)
Pyrazine	*Bacillus subtilis*	Fermented soyabean	Zhang et al. (2020a)

Table 2
Food sources and chemical structure of some Lactones types.

Lactones Types	Chemical Structure	Food Sources
δ-Hexalactone		Fruit and milk products
γ-Octalactone		Yoghurt, peaches, oranges and sweet fortified wines
δ-Decalactone		Tea, blue cheese, tobacco, mango, strawberry and butter
δ-Undecalactone		Milk products
γ-Dodecalactone		Milk products and coconut
Massoia lactone		Tobacco, wine and molasses
Jasmine lactone		Jasmine and gardenia flowers, tobacco and tea
6-Amyl-α-pyrone		Animal foods, peach and heated beef

Decalactone from the oil of *R. communis* has been reported to be produced by the microorganisms such as *Aspergillus niger*, *Cladosporium suaveolens,* and *Pichia etchelisii* (Prabakaran et al., 2020) Some microbial species such as *Monilia fructicola*, *Rhodotorula glutinis,* and *Sporobolomyces odorus* have been used to report comparatively lower product yields (Bhari and Singh, 2019). The oleaginous yeast (*Yarrowia lipolytica*) engineered recently by **Marella and co-workers,** in which it has been used by beta(β)-oxidation to hydroxylate fatty acids (FAs) and to shorten-chain preferentially 12 or 10 carbons (Marella et al., 2020). The engineered strains have shown that γ-Dodecalactone and δ-Decalactone from oleic and linoleic acid respectively yield fourfold higher levels than the wild strain, thereby paving the way for higher lactone production by fermenting available fatty feedstocks. The dairy products are particularly attractive for the buttery coconut, and milky flavours of these microbiologically-based lactones (Marella et al., 2020).

The fragrance of coconut (*C. nucifera*) is due to 6-pentyl-2-pyron (6-PP) which has been reported to be a key VFC in the cultures of *Trichoderma viride*. The γ-dodecalactone and δ-Decalactone have been converted from coriolic acid and ricinoleic acid (Siddiquee, 2017; Khan et al., 2020). *N*-octanoic acid (caprylic acid) is found in coconut oil which has been fermented by *Mortinella* spp. to produce octalactones. Whereas, 11-hydroxy palmitic is found in sweet potatoes (*Ipomoea batatas*) which has also been reported to produce δ-Decalactone by fermentation of yeast species (Vandamme and Soetaert, 2002).

Previously, De Aráujo et al.(2002) evaluated the production of an unsaturated lactone 6-pentyl-a-pyrone (6-PP) with a strong coconut-like aroma, using both liquid and solid substrates in solid state fermentation (SSF) process where they used sugarcane bagasse as a substrate for growth and aroma production. In another approach, using mixed cultures of Lactobacillus acidophilus and Pediococcus pentosaceus, semisolid maize-based medium was utilized to produce flavour compounds like diacetyl, butyric acid and lactic acid by Escamilla-Hurtado et al. (2005).

2.2. Carboxylate esters

Natural microorganisms for ester synthesis are well known and have traditionally been used in food production, such as lactic acid bacteria (LAB) and yeast. Of these esters, volatile esters are the most important aromas in fermented foods, including beer, dairy, and wine products. Ester produces a pleasant, fruity fragrance at low concentrations, but is also considered to be off-tasting when found in significant amounts. Ethylacetate is the highest volatile ester in food. The concentration of such volatile ester in dairy products varies between ~ 50 and 100 mg/L (Wang et al., 2016) and in

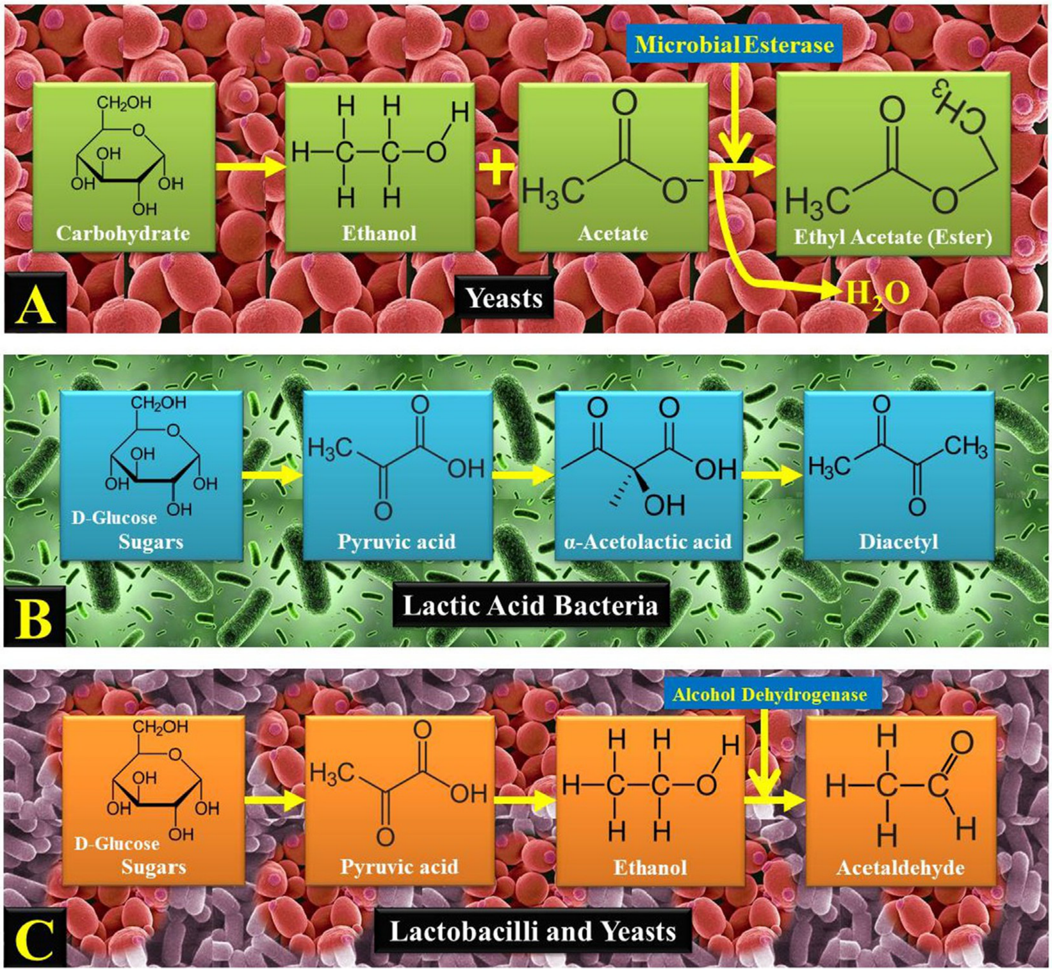


Fig. 4. Synthesis of different microbial VFCs. (A) Ester (ethyl acetate) synthesis from carbohydrate through yeasts, (B) Diacetyl synthesis from carbohydrate in LAB, (C) Acetaldehyde synthesis from carbohydrate in lactobacilli and yeasts.

beer and wine between ~ 0 and 60 mg/L (Daniel et al., 2015). There are several more volatile esters, including ethyl hexanoate, isoamyl acetate, and phenylacetate, but concentrations of more than 1 mg/L have not been observed (Dzialo et al., 2017). These amounts lying at or just above the threshold for identification by human beings impair the scent of food items significantly (Dzialo et al., 2017). While there are some exceptions, including the mass production of acetate-generated yeast or wax ester production by *Euglena gracilis* (Inui et al., 2017), the amount of natural ester from microorganisms is usually small. Under anaerobic conditions, wax esters have been documented to accumulate as much as 65% of the dry cell weight (Inui et al., 2017). Ethylacetate from sugars or ethanol can be synthesized by yeasts including *Cyberlindnera jadinii*, *Kluyveromyces marxianus,* and *Wickerhamomyces anomalus* (Fig. 4 **A**) (Fan et al., 2019; Zhang et al., 2020b). There are also other enzyme groups that can form ester but for ester synthesis, they have not been used widely (Xu et al., 2020).

2.3. Alcohols

Unsaturated alcohols have been used in food ingredients with a distinctive scent. Many types of yeast contain complex alcohols with a long chain of organoleptic properties (Wang et al., 2019a). The batch of fermented wine with *Saccharomyces cerevisiae* was immobilized by **Liang and coworkers** with a fine cellulose material, who produced a rose-like scent, 2-phenyl ethanol, in a fermented wine (Liang et al., 2020). This offers an alternative microbial path for the synthesis of alcohol, which is usually isolated from rose petals or chemically synthesized. *Hansenula anomala*, *K. marxianus*, and *S. cerevisiae* have been identified for the production of 2-phenylethanin from 2-phenylalanine (Chantasuban, 2016). Noteworthy, *K. marxianus* was engineered by **Kim and coworkers** to overexpress genes that encode enzymes (such as alcohol dehydrogenase and phenylpyruvates decarboxylase) from *S. cerevisiae* that contribute to the overproduction of 2-phenylethanol from glucose (Kim et al., 2014). *S. cerevisiae* is an alternative ethanol synthesis microorganism to *Zymomonas mobilis*. The growth and synthesis of ethanol from four isolates were contrasted with the growth and synthesis of the efficient strain *Z. mobilis* (NRRL B-14023) at different temperatures in order to detect the thermotolerant strain of *Z. mobilis* (Xia et al., 2019). In *Z. mobilis*, glyceraldehyde-3-phosphate-to-pyruvate, and pyruvate-to-ethanol pathways, the ethanol production route of glucose, consisting of the Entner-Doudoroff path, provides the majority of ATP needed for cell activity for approximately one mole of ATP per mole of glucose (Xia et al., 2019).

2.4. Ketones

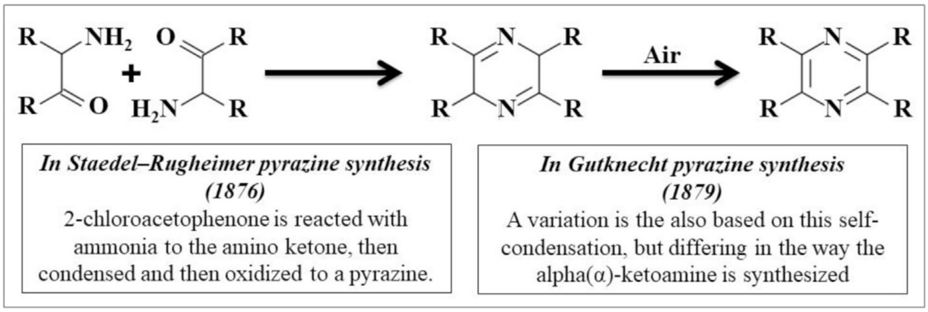
Ketones are carbonyl molecules (=C = O) that trigger a lot of natural flavours and smell. Several saturated as well as unsaturated aromatic, aliphatic, and cyclic ketones have been reported from the cheese (Caron et al., 2021; Ianni et al., 2020). Among them, unusually C_5-C_{11} numeric ketones, such as 2-alkanones along with secondary alcohols and free fatty acids (FFAs), which may have their distinctive aromas in *Penicillium*-ripened cheese (Caron et al., 2021). Diacetyl is known as a butter-flavoured vicinal diketone, and is therefore used for the simulation of butter-like and other milky flavours (Wang et al., 2019b). It is produced in dairy foods by various microorganisms including lactic acid bacteria (LAB) (Wang et al., 2016; Wang et al., 2019b). In Fig. 4 **B**, the biosynthesis of diacetyl in LAB from carbohydrates is depicted. It is interesting to note that the metabolically engineered *Enterobacter clocae* provided high levels of diacetyl (1.45 g/L), while diacetyl and acetaldehyde were produced by yeasts *Candida tropicalis* strain D15 in the whey-based medium (Rosca et al., 2016). The essential components of the cooked flavour of the butter-containing baked food are methyl ketones. Methyl ketone precursors occur as alkanoic acids in fresh butter with no aroma features. However, they are converted into methyl ketones, which are the main VFCs in cooked and heated foods containing butter. These VFCs are formed by *A. oryzae*, *A. niger*, *A. bisporus*, *Penicillium roquefortii,* and *T. viride*. The mechanism of β-oxidation of FAs can be used to rapidly produce methyl ketones in microbes (Sharma et al., 2020).

2.5. Aldehydes

Vanillin is a 4-hydroxy-3-methoxybenzaladehyde and is considered a very effective VFC used in food for industrial purposes. The extraction of this VFC vanillin from vanilla pods is difficult due to labor-intensive and costly production. Due to increased consumer demand for natural vanillin, there is no need for chemically synthesized vanillin. As a result, several groups of researchers have obtained vanillin from essential oils by the microbial conversion of eugenol and isoeugenol (Ashengroph and Amini, 2017). Surprisingly, lignocellulosic obtained from agricultural residues have been discussed as a rich source of ferulic acid in a recently published report by Sharma and coworkers (Sharma et al., 2020). Furthermore, the use of ferulic acid has also been addressed in vanillin synthesis through microbial or enzyme transformations (Sharma et al., 2020). However, this procedure requires the synthesis of vanillin in which ferulic acid is released from lignocellulosic waste by enzyme or chemical intervention. Some bacteria and fungi may transform the released ferulic acid into vanilla, vanilla, and protocatechuic acid. The role of ferulic acid in the field of bioflavour production has therefore been recognized as a precursor to vanillin synthesis (Tang and Hassan, 2020; Sharma et al., 2020). Vanillin has been biotransformed into ferulic acid by numerous microbial species (Tang and Hassan, 2020), including *Actinomycetes* spp., *Amycolatopsis* spp., *Aspergillus* spp. (*A. niger*), *Bacillus* spp. (*B. coagulans*, *B. licheniformis,* and *B. subtilis*), *Corynebacterium* spp. (*C. glutamicum*), *Debaryomyces* spp. (*D. hanseni*), *Escherichia* spp. (*E. coli*), *Halomonas* spp. (*H. elongata*), *Pseudomonas* spp. (*P. fluorescens* and *P. putida*), *Pycnoporus* spp. (*P. cinnabarinus*), *Rhodococcus* spp., *Rhodotorula* spp. (*R. rubra*), *Saccharomyces* spp. (*S. cerevisiae*), *Schizophyllum* spp. (*S. commune*), and *Streptomyces* spp. (*S. halstedii*, *S. sannanensis*, and *S. setonii*). For the synthesis of cherry and fruity flavour, benzaldehyde is the second largest aldehyde next to the vanillin. It can be obtained from *P. armeniaca* (apricots), but the procedure results in unwanted hydroxycinnamic acid accumulation. Additionally, microbial synthesis of benzaldehyde from phenylalanine may be considered as "natural" without undesirable by-products. In this context, the engineered *Pseudomonas taiwanensis* strain has been found to synthesized benzaldehyde in supplemented medium of glucose or glycerol (Otto et al., 2020). In fermented milk like yoghurt, acetaldehyde is the key flavouring compound formed by several *Lactobacillus* sp., further few types of yeast were also found to synthesize acetaldehyde (Dan et al., 2019; Rosca et al., 2016**).** In Fig. 4 **C**, the biosynthesis of acetaldehyde from carbohydrates is depicted.

2.6. Pyrazines

Pyrazines are heterocyclic molecules that contain nitrogen and produce nutty and roast flavours (Mortzfeld et al., 2020). The main factors for green flavours in sauvignon Blanc wines are 3-isopropyl-2-methoxy pyrazine and 3-isobutyl-2-methoxy pyrazine. Furthermore, there are also several other essential chemical compounds which have been considered as flavour enhancers. For example, 2,3,5-trimethyl pyrazine, 2-acetyl-3-methoxy pyrazine, 2-methyl-3-isobutyl pyrazine, and 2-methyl-3-methoxy pyrazine improve the flavour of chocolate, almonds, bell pepper, and toasted corn (Mortzfeld et al., 2020; Guo et al., 2021). There are many available approaches used for the organic synthesis of pyrazine and its derivatives. Some of the proposed approaches are the oldest, and some are recent. The reactions used for synthesis in the oldest methods are Staedel–Rugheimer pyrazine synthesis (1876) and Gutknecht pyrazine synthesis (1879) still in use, with variations in each other (Fig. 5). Historically, the first microorganism reported for pyrazine synthesis was *Bacillus subtilis* (Zhang et al., 2020a). Previously, tetramethylpyrazine (TMP) and 2,5-dimethylpyrazine (2,5-DMP) were synthesized from acetoin, D-glucose, and L-threonine using the strain *B. subtilis* 168 (Zhang et al., 2019). In addition, pyrazines synthesis from amino acids (AAs) has also been reported using *Corynebacterium glutamicum* (Eng et al., 2020). Nutty and chocolate flavouring chemical pyrazines have recently been synthesized by Fadel and coworkers using *C. glutamicum* grown on soyabean (*Glycine* max) with enriched lysine and threonine medium (Fadel et al., 2018). Maillard reactions can also produce pyrazines in conventional cooking and roasting. However, pyrazines have not been synthesized due to advances in cooking techniques, such as the use of microwave ovens. We can therefore conclude that roast flavour as food additives must be provided with natural pyrazines.



In Staedel–Rugheimer pyrazine synthesis (1876)
2-chloroacetophenone is reacted with ammonia to the amino ketone, then condensed and then oxidized to a pyrazine.

In Gutknecht pyrazine synthesis (1879)
A variation is the also based on this self-condensation, but differing in the way the alpha(α)-ketoamine is synthesized

Fig. 5. Pyrazine synthesis by condensation reaction.

LABs are able to synthesize different flavours by catabolism amino acids. Initially, the amino acids are involved in dehydrogenation and transamination reactions and forms α-ketoacids, a compound which have a primary effect on flavour amount and type. Moreover, α-ketoacids are converted in aldehydes through decarboxylation reaction (Petrovici and Ciolacu, 2018). In one of the researches, development of phenylacetaldehyde (with honey-like aroma) was identified by *Lb. helveticus, Lb. plantarum* UC1001, and *S. thermophilus* from catabolism of methionine (Siragusa et al., 2011). The same strains also showed synthesis of propionic acid from catabolism of threonine. Similarly, the biosynthesis of the diacetyl by some Lactobacillus strains from aspartate has been reported by Garde et al. (2007) while Zuljan et al. (2016) showed the formation of α-keto-β-methyl valerate from isoleucine catabolism.

3. Antimicrobial activities and action mechanism of flavour compounds

All the antimicrobial compounds have not yet been studied for their specific mechanisms for action. Unlikely 2-(*E*)hexenal appears to behave as a surfactant but probably penetrates across the plasma membrane with passive diffusion. The alpha(α)- and beta(β)-an unsaturated movement of aldehyde while within cells react with biologically significant nucleophilic classes. This aldehyde movement has mostly reacted by 1.4 additions in physiological conditions with sulfhydryl groups (Hayashi et al., 2019). Sulfhydryl groups are considered to play an important function in living cells in protein, and lower-molecular compounds such as glutathione (Li et al., 2020b). The mode of action of the bioactive compounds of spices, herbs, and plants are more complex to assume since they also have varying quantitative and qualitative ratios of essential oils. They may vary greatly from the target microorganisms and the minimum inhibitor concentrations in their microbicidal and microstatic effects (Merveille et al., 2017). The techniques of analyzing antimicrobial activities and, in particular, the protocols followed for the extraction, diffusion, and dilution of chemical compounds may be due to certain inconsistencies in the bioactivity assessment of those chemical compounds. Essential oils are combinations of chemicals compounds that also have low water solubility and high hydrophobicity (Sarıcaoglu and Turhan, 2020). In the previous study, **Janssens and coworkers** evaluated *Paenibacillus* sp. AD87 which demonstrated antifungal activity because of the 2,5-*bis*(1-methylethyl)-pyrazine during a co-culture with *Burkholderia* sp. AD24. In addition, *E. coli* and mammalian cells were used to decipher a potential mode of action with transcriptional reporter tests. Strains of mammalian and bacterial luciferase reporter were also used to elucidate 2,5-*bis*(1-methylethyl)-pyrazine antimicrobial and toxicological effects. 2,5-*bis*(1-methylethyl)-pyrazine had a good reaction to DNA damage at elevated exposure levels (Janssens et al., 2019). During a 15 days storage time, at 4 ± 1 °C, the mixture of vanillin and chitosan coating had an influence upon the microbiota composition and duration of turbot filets (*Scophthalmus maximus*). The relative abundance of the *Lactobacillaceae* and *Pseudomonadaceae* had decreased significantly following vanillin and chitosan treatment due to the growth inhibition of possible bacteria, particularly spoilage bacteria, and the rich end of storage body diversity (Li et al., 2020a). Moreover, *Photorhabdus temperata* produced benzaldehyde showed a strong antioxidant activity (AOA) and a maximum AOA at 8 mM compared to a control of 52.9 %. MIC values of 6 mM to 10 mM for bacterial strains and 8 mM to 10 mM for fungal strains were measured for antimicrobial activity (Ullah et al., 2015).

Strains of LAB and bifidobacteria could produce diacetyl in up to 30 mg/mL concentrations and had a potential to exhibit antimicrobial activities, especially against Gram-negative bacteria (such as i, *Pseudomonas aeruginosa*, *Salmonella typhi, Pasteurella multocida*, *Klebsiella rhinoscleromatis,* and *Bartonella* sp.,) as well as against fungi (Lew and Liong, 2013; Patel and Shah, 2014). Another direction of using diacetyl is related to active packaging systems where the controlled release of volatile antimicrobial compounds is possible through packaging material. In this context, in conjunction with 20% $CO_{2,}$ effects of diacetyl were evaluated on the quality of ground beef while using it in modified-atmosphere packaging. It was associated with the fresh colour and odour of the products as well as a delayed spoilage of product (Williams-Campbell and Jay, 2002).

4. Microbial flavours compounds in food

Fermentation is a common way of preserving and preparing foods. In different foods, it can produce specific aromas and flavours. Microbial flavours are one of the food's most significant qualities and are closely linked to consumer product approval. In the past decades, the interest in the biotechnological production of VFCs has increased in various ways to achieve these compounds as this technique has been seen as a sustainable means of providing the food industry with natural additives (Dan et al., 2019; Paulino et al., 2021). Due to their mild environments, their biotechnological synthesis of VFCs is not subject to possible toxic catalysts and the problems of waste treatment are considered an ecologically safe solution. Furthermore, agro-residues can be used as a substitute, ecologically as well as economically beneficial raw materials for this bioprocess. The waste of cellulose, lignocellulose, and starch can also be used for the synthesis of VFCs like aldehydes, alcohols, ketones, FAs, esters, terpenes, pyrazines, and lactones. Furthermore, industrial fermentation does not require extractive considerations for the processing of flavours (Try et al., 2018; Sharma et al., 2020). Different volatile compounds have been detected through gas chromatography and other combined treatments based on the type of fermenting microorganisms and food products (Table 3**).**

The following section discusses the VFCs of enzymatic and microbial origin, as well as the progress in their potential and commercial use in food.

4.1. In dairy products

Traditional fermented foodstuffs and drinks are relatively like complex microbial habitats which can be used as microbial models to explain the interaction of microbes in natural ecosystems because of the diverse essence and patterns of the kefir fermentations (Misihairabgwi and Cheikhyoussef, 2017). The previous researches have revealed the relationship between different microorganisms and their associated pathways for synthesis of VFCs, and established multiple genes responsible for the alleged wellness related to the protection of the gut used by kefir (Walsh et al., 2016; Misihairabgwi and Cheikhyoussef, 2017). This knowledge can ultimately be used to refine the fermentation mechanisms, flavours, and health properties of this and other fermented foods, in addition to providing an important fundamental insight into microbial interactions. In kefir milks formed from each of the three kefir grains, thirty-nine volatile aroma compounds were detected and semi-quantified. This included aldehydes (7), ketones (9), esters (6), alcohols (8), carboxylic acids (5), and sulfur-containing (2) compounds. In addition to acetone, butanone, heptanal, heptanol, hexanal, 1-pentanol, and pentanal, the amounts of all reported VFCs rose during storage time (Walsh et al., 2016).

Table 3
Presence of volatile compounds in different food products by gas chromatograpgy.

Type of Food Product/ Sample	Details of GC Column	Major Finding(s)	Reference
Suan-zuo-yu	7890B gas chromatography coupled to 5977B mass selective detector with a VF-WAXms capillary column (30 m length × 141 0.25 mm inner diameter × 0.25 μm film thickness)	GC–MS showed a complete identification of 80 VFCs and a significant increase in aldehydes, alcohols and esters, which mainly led to the flavour of the product by LAB fermentation.	Wang et al. (2020b)
Ewes' milk cheese	DB5 capillary column, 0.32 μm internal diameter, 1 μm film thickness, 60 m long	The levels of several volatile organic compounds were significantly ($P < 0.05$) lower in control cheese than in cell-free extracts-supplemented cheeses. All cheeses manufactured by adding multiple CFEs exhibited higher scores ($P < 0.05$) for internal structure, juiciness, and acid taste than control samples.	Calasso et al. (2017)
Sliced cooked pork	ZB-WAXplus polyethylene glycol capillary column, 0.25 mm internal diameter; 0.50 μm film thickness, 60 m long	At the end of the storage period, 500 and 600 MPa samples contained higher levels of branched-chain aldehydes, ethanol, diacetyl, acetoin, and 2,3-butanediol whereas control and 400 MPa samples showed higher levels of fatty acids and ethanol and ethyl acetate esters.	Rivas-Cañedo et al. (2011)
Pecorino Abruzzese cheese	CP-Wax 52 CB polyethylene glycol coated, 0.32 mm, 1.2 mm film thickness, 50 m long	The analyses of volatile compounds revealed the production of diacetyl, ethanol, and acetoin after 15 days at 10 °C, with important differences among the Enterococcus sp.	Serio et al. (2010)
Morcilla de Burgos	HP-5MS capillary column, 5% phenyl methyl silicone, 320 μm, 1.0 μm, 60 m long	W. viridescens samples showed greater amounts of alcohols (ethanol) and ketones (acetoin and diacetyl) whereas L. mesenteroides samples were richer in aldehydes (hexanal) and acids (acetic).	Diez et al. (2009)
Cheese	HP-INNO-WAX polyethylene glycol capillary column, 250 μm, 0.5 μm, 60 m long	The mixture of L. lactis IFPL326 led to the highest formation of leucine-derived volatile compounds like 3-methylbutanal, 3-methyl-1-butanol and 2-hydroxy-4-methyl pentanoic acid methyl ester through aminotransferase activity with IFPL730	Amárita et al. (2006)

The main routes of VFCs synthesis in cheese are due to lactate and lactose metabolism. The lactate may be transformed into different compounds that lead towards the flavour of the cheese in the first path, which completely depends on the variety of cheese, employed microflora, and conditions of ripening (Ianni et al., 2020). The other route produces fat-derived chemical compounds, such as esters, FFAs, ketones, and lactones, produced by lipolysis, lipid oxidation reactions with low aroma levels (Thierry et al. 2017). The aroma of cheese is due to VFCs produced by the action of the enzyme during the ripening.

Cheese from the Uyghur Autonomous Region of China, a characteristic handmade fermented milk food is known as Kazak cheese (Zheng et al., 2021). Recently, Zheng and coworkers investigated bacterial microbiota and VFCs during the milk fermentation of Kazak cheese. Headspace solid-phase microextraction (Hs-SPME) and Illumina MiSeq sequencing technologies were used in their investigation as analytical instrumentation coupled with gas chromatography/mass spectrometry (GC–MS). Dominant populations such as *Lactococcus* and *Lactobacillus* were reported during the fermentation of the milk. The relation between the flavour dynamics and the succession of the microbiome was defined based on the bi-directional orthogonal partial least squares (O_2PLS) in which eight genera of bacteria were identified as the main functional microbes for the synthesis of flavour (Zheng et al., 2021).

. Since the flavour synthesis of natural milk fat, interest in the application of biocatalysts has gradually increased. Lipases are a class of enzyme which have been most studied as biocatalysts for the synthesis of flavour from bovine milk fat (Omar et al., 2016; Kendirci et al., 2020). In earlier studies of Omar and coworkers, anhydrous milk fat (AMF) and anhydrous buffalo milk fat (ABMF) were hydrolyzed using *Thermomyces lanuginosus* immobilized (TL-IM) lipase, Lipozyme-435, and Novozyme-435 (Omar et al., 2016). In addition, SPME and GC–MS were used to study the VFCs of AMF and ABMF. Omar et al. (2016) compared these VFCs at three intervals of hydrolysis. After the lipolysis of AMF and ABMF, the Novozyme-435 and Lipozyme-435 produced the highest hexanoic and butanoic acids as well as other VFCs, followed by TL-IM. Rancimat-743 evaluated hydrolyzed materials for oxidative stability, both of which showed that butter oil-treated for AMF and ABMF was relatively more stable in Lipozyme-435 and TL-IM compared with Novozyme-435. Lipozyme-435 was found not to induce additional oxidation effects indicating that Lipozyme-435 was stable during 24 h, at 55 °C, for both AMF and ABMF butter oil-treated (Omar et al., 2016).

Calasso et al. (2017) carried out measurement of volatile compounds produced in Ewes' milk cheese through gas chromatography. Authors stated that the levels of several volatile organic compounds were significantly ($P < 0.05$) lower in control cheese than in cell-free extracts (CFE)-supplemented cheeses. All cheeses manufactured by adding multiple CFEs exhibited higher scores ($P < 0.05$) for internal structure, juiciness, and acid taste than control samples. Similar to this, in a previous approach, in Pecorino Abruzzese cheese the analyses of volatile compounds observed the production of diacetyl, ethanol, and acetoin after 15 days during storage at 10 °C with important differences among the Enterococcus sp. (Serio et al., 2010).

4.2. In meat products

More than 200 different volatile compounds have been identified from fermented meat items (Sharma et al., 2020). Changes in physicochemical, microbiological, and sensory properties are caused by storage. A range of studies has been conducted to address the effect of VFCs responsible for the production of ripened aroma (Sidira et al., 2016; Perea-Sanz et al., 2019, 2020; Silva et al., 2020). Perea-Sanz et al. (2019) described short vacuum storage times and a modest nitrate reduction (15%) in fermented sausages linked to odor-producing compounds (2,3-pentanedione, 3-hydroxy-2-butanone, ethyl octanoate, and ethyl-3-methylbutanoate) and buttery/cheesy odor (ethyl-2-hydroxypropanoate and 2,3-butanedione). While in the freshness of cured pork loins, Silva et al. (2020) reported that the loss was mainly due to decreased aromatic note values (especially the smokiness and cure) and to the presence of spoiled characteristics, primarily the aroma of sauce/vinegar and acidic flavour identified. According to a reduced ratio of respondents, *Listeria monocytogenes* inoculated in the cured pork loins slices did not result in a reduction in the freshness of pork slices.

In addition, the effect of *Debaryomyces hansenii* inoculation on the production of fragrance was examined to reduce the ingoing levels of nitrite (NO^{-2}) and nitrate (NO^{-3}) in dry fermented sausages. Different drying periods have been examined for modifications in physicochemical and microbiological parameters, flavours, and VFCs (Perea-Sanz et al., 2020). The reduction in NO^{-2} and NO^{-3} did not seem to affect microbial development, but on their metabolic function. *D. hansenii* inoculation, which led to the generation of strong compounds such as ethyl ester and 3-methyl butanal, had a beneficial impact on the aroma profile of sausage (Perea-Sanz et al., 2020).

High counts of LAB were mildly affected by the diameter of dry fermented sausages of the Milan type, whereas higher Staphylococci concentrations were found in small sausages. The diameter had a significant effect on the production of VFCs like aldehydes (mainly hexanal) and ketones (acetone, 2,3-butandione, 2-butanone, and 3-hydroxy-2-butanone,), which showed the major variations. Even the appearance of the indigenous *Lactobacillus sakei* in the saucers inoculated with pediococci showed a less obvious influence on the starter cultures (Montanari et al., 2018). The starter culture has a direct impact on certain key process parameters (acidification and fermentation rate) and VFCs generation for all forms of fermented foods.

For the reason that aldehydes send out green grass, nutty, candy and cheese odor and have low threshold values, aldehydes are considered as essential compounds to the flavor development of fermentation meat (Dajanta et al., 2011).

4.3. In sea food products

One of the essential quality characteristics of fermented fish is its distinctive flavour. The studies on the formulation in flavours of fermented fish products have been focused primarily on isolation, purification, and characterization of VFCs and their biosynthesis process. The breakdown of protein substrates with the effect of enzymes obtained from both the microbes and fish have also been described to produce a specific flavour during the spontaneous fermentation of fish (Marti-Quijal et al., 2020). In a recent report, the fermentation was classified into two phases during the Mandarin fish fermentation based on microbiota changes: early, 1st-3rd, and late, 4th-7th, days. The typical VFCs of Mandarin fish fermentation were anethole, indole, linalool, piperitone, 2-methyl-3-octanone and 1-octen-3-ol (Yang et al., 2020). The large chain protein, myosin, and actin were decreased during the fermentation process of Suan-zuo-yu by LAB. GC–MS showed a complete identification of 80 VFCs and a significant increase in aldehydes (6), alcohols (6), and esters (6), which mainly led to the flavour of Suan-zuo-yu (Wang et al., 2020b).

Previously, GC–MS was also used for the analysis of VFCs (Wang et al., 2016**, 2017**). In 2017, GC–MS was used to identify acids, alcohols, aldehydes, esters, furans, hydrocarbons, ketones, and nitrogen-containing compounds (Wang et al., 2017). These were the main VFCs produced by the process of fermentation of fish. Wang and coworkers investigated fermented fish flavour and showed that *S. cerevisiae* 152 had degraded aromatic AAs (phenylalanine) and branched-chain AAs (leucine, isoleucine, and valine) to produce phenyl-ethanol, 2-methyl-butanol, 2-methyl-propanol, and 3-methyl-1-butanol. Furthermore, degradation of leucine and phenylalanine were also reported, resulting in the synthesis of phenylethanol and 3-methyl-1-butanol from *Lactobacillus pentococcus* 22 and *Lactobacillus plantarum* 120, respectively (Wang et al., 2017).

Esters are essential VFC in Suanyu fermentation that is indirectly implicated in FFA metabolism, contributing to the biosynthesis of esters due to esterification and alcoholic response. LAB was found to encourage acetate compounds production whereas *Staphylococcus* and yeast would promote ethyl compounds production (Sidira et al. 2016). As described above, microflora metabolic activities can produce a range of volatility, which can contribute eventually to the taste and consistency of metabolism of AAs and FAs. The addition of metabolic flexibility and microbial diversity may also provide the opportunity for innovative and enhanced products.

LABs are beneficial microorganisms for fermentation which could generate bioactive peptides and produce vitamins in fermented foods like fishes (**Şanlier et al., 2019;** Patel et al., 2013). In a study of Wang et al. (2020b), the levels of *Weissella* and *Lactobacillus* gradually increased from 0.311% to 46.00% suggesting that LAB play a vital role in fermentation of a traditional Chinese fermented fish product Suan-zuo-yu. Authors stated that increase in *Staphylococcus* was accompanied with the increase of esters while *Macrococcus* able to hydrolyze proteins and lipids was also presented throughout the fermentation process. In a previous study, *Macrococcus* was also detected in Chouguiyu, a kind of traditional Chinese fish product by Dai et al. (2013); Marui et al. (2014) found *Lactobacillus* and one *Weissella* sp. as a predominating bacteria from pa-*som*, a traditional fermented fish product in Laos.

Acetaldehyde plays a role in the rate of fermentation and the quality of wine. In a recent investigation, higher acetaldehyde levels were found in wines inoculated with *Saccharomyces cerevisiae*, exposed to high sulphur dioxide (SO_2) levels, and fermented at higher temperatures (October 2020). There was a direct correlation between total ADH activity and total acetaldehyde production of *S. cerevisiae* yeasts.

5. Factors affecting production of microbial flavours

The compositions of growth media (including nitrogen and carbon source types), temperature, mineral composition, and level of aeration have a great influence on the biosynthesis of flavours by any microbial strain. For an instance, Paterson and Piggott (2006) stated that the addition of sucrose in the culture media stimulates the flavour biosynthesis for LABs and yeasts. With respect to this**,** Di Cagno and co-workers (2009) supplemented the tomato juice with sucrose and subsequently subjected to LAB fermentation in order to encourage the flavour production and also to lessen the intrinsic acidic flavour of tomatoes. Earlier, Cheetham (1999) in a milk or whey medium supplemented with citric acid as a precursor, a high diacetyl concentrations of up to 14 g/L have been stated for a patented process making use of *Streptococcus cremoris* and *S. diacetylactis*.

Similarly, the presence of oxygen strongly affect the growth of microbial strain and hence, the flavour biosynthesis. Under aeration conditions, *Lb. casei* leads to higher biosynthesis of diacetyl in Cheddar cheese than an anaerobic starter culture (Reale et al., 2016). On the other side, *E. faecium* FAIR-E 198 strain showed diacetyl biosynthesis only in aerobic conditions (De Vuyst et al., 2011).

The fermentation temperature strongly influences biosynthesis of flavour by microorganism. For example, *Lb. rhamnosus* ATCC 7469 biosynthesized diacetyl and acetoin within a temperature interval of 22–45 ℃ from citrate (De Figueroa et al.,) The maximum biosynthesis of diacetyl was observed in the temperature interval between 30 and 37 ℃ within 48 h; as compared to 22℃, the level of the diacetyl and acetoin was 4.1 time higher at 37℃. This effect is chiefly associated with the enzymatic activities in the microbial cell.

The presence of minerals also affects flavour production in microbial cells. In *Lb. plantarum* van Kranenburg et al. (2002) characterized two manganese transport systems which are implicated in mineral uptake and convert phenylalanine to benzaldehyde by initiation of a pyridoxal 50-phosphate-dependent aminotransferase. Further, in the presence of oxygen and manganese the obtained phenyl-pyruvate is further chemically transformed to benzaldehyde. In another research, it was observed that magnesium and manganese sulphate enhanced biomass and aroma development both of different 52 yeasts by obtaining 3.58 mg/L diacetyl for *Candida globosa* and 96.05 mg/L acetaldehyde for *Candida lipolytica* (Rosca et al., 2016).

In depth knowledge of the metabolism in microorganism has led to develop innovative strategies for engineering microbial strains with high flavour production in recent years. In a fibrous-bed bioreactor running under fed batch conditions immobilization of *Propionibacterium acidipropionici* ATCC 4875 led to 72 g L-1 propanoic acid (Suwannakham and Yang, 2005) while in separate investigation, knocking out the *ack* gene (acetate kinase) diminished unwanted acetic acid formation by 14% (Suwannakham et al., 2006).

6. Concluding remarks

The biotechnological synthesis of VFCs has gained popularity because of market demands for natural products and enhanced economic benefits. Low-cost natural precursors can be converted by microbes and their enzymes into costly VFCs and microbial synthesis methods benefit against conventional methodologies. Bacterial metabolisms can be used to produce different biocatalytic instruments to produce natural and fragrant value-added compounds and chemical synthesis from inexpensive plant biomass. Future directions to produce natural VFCs should be opened up by biotechnological advances. However, there should be solved certain concerns such as parent compound's toxicity, product toxicity, targeted gene expression and recombinant bacterial strain's physiological stability, in order to obtain costly "natural" flavours from genetically modified microorganisms (GMOs). Furthermore, the challenges faced by GMOs should also be addressed.

Contribution of the authors

AKN, DKV, and STGA have conceptualized, interpreted, corrected, and made scientifically sound final versions of the manuscript; while, MT, ARP, NS, SS, DB, GLU, and CAN have provided technical suggestions and corrections for the final version of the manuscript. Funding acquisition has been provided by CAN. All authors critically reviewed and approved the final version of the manuscript for submission.

Declaration of Competing Interest

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

References

Al-fekaiki, D.F., Niamah, A.K., Al-Sahlany, S.T.G., 2017. Extraction and identification of essential oil from *Cinnamomum zeylanicum* barks and study the antibacterial activity. Journal of Microbiology, Biotechnology and Food Sciences 9 (6), 312–316. https://doi.org/10.15414/jmbfs.2017/18.7.7.312-316.

Amárita, F., De La Plaza, M., De Palencia, P.F., Requena, T., Peláez, C., 2006. Cooperation between wild lactococcal strains for cheese aroma formation. Food Chemistry 94 (2), 240–246. https://doi.org/10.1016/j.foodchem.2004.10.057.

Ashengroph, M., Amini, J., 2017. Bioconversion of isoeugenol to vanillin and vanillic acid using the resting cells of *Trichosporon asahii*. *3*. Biotech 7 (6), 358. https://doi.org/10.1007/s13205-017-0998-9.

Ayseli, M.T., Ayseli, Y.İ., 2016. Flavors of the future: Health benefits of flavor precursors and volatile compounds in plant foods. Trends in Food Science & Technology 48, 69–77. https://doi.org/10.1016/j.tifs.2015.11.005.

Bhari, R., Singh, R.S., 2019. Microbial Production of Natural Flavours. In: Joshi, V.K. (Ed.), Technology of Handling, Packaging, Processing, Preservation of Fruits and Vegetables: Theory and Practicals'. New Delhi, Publishing Agency, India, pp. 767–813.

Calasso, M., Mancini, L., De Angelis, M., Conte, A., Costa, C., Del Nobile, M.A., Gobbetti, M., 2017. Multiple microbial cell-free extracts improve the microbiological, biochemical and sensory features of ewes' milk cheese. Food Microbiology 66, 129–140. https://doi.org/10.1016/j.fm.2017.04.011.

Caron, T., Piver, M.L., Péron, A.-C., Lieben, P., Lavigne, R., Brunel, S., Roueyre, D., Place, M., Bonnarme, P., Giraud, T., Branca, A., Landaud, S., Chassard, C., 2021. Strong effect of Penicillium roqueforti populations on volatile and metabolic compounds responsible for aromas, flavor and texture in blue cheeses. International Journal of Food Microbiology 354, 109174. https://doi.org/10.1016/j.ijfoodmicro.2021.109174.

Chantasuban, T., 2016. Assessing the Wine Yeast *Metschnikowia pulcherrima* for the Production of 2-Phenylethanol PhD Dissertation. University of Bath, United Kingdom.

Cheetham, P.S.J., 1999. In: Encyclopedia of bioprocess technology: fermentation, biocatalysis, and bioseparation. Wiley, New York, p. 1004.

Dai, Z., Li, Y., Wu, J., & Zhao, Q. (2013). Diversity of lactic acid bacteria during fermentation of a traditional Chinese fish product, Chouguiyu (stinky mandarinfish). Journal of food science, 78(11), M1778-M1783. https://doi.org/10.1111/1750-3841.12289

Dajanta, K., Apichartsrangkoon, A., Chukeatirote, E., & Frazier, R. A. (2011). Free-amino acid profiles of thua nao, a Thai fermented soybean. Food Chemistry, 125 (2), 342-347. https://doi.org/10.1016/j.foodchem.2010.09.002.

Dan, T., Ren, W., Liu, Y., Tian, J., Chen, H., Li, T., Liu, W., 2019. Volatile flavor compounds profile and fermentation characteristics of milk fermented by *Lactobacillus delbrueckii* subsp. *bulgaricus*. Frontiers in Microbiology 10, 2183. https://doi.org/10.3389/fmicb.2019.02183.

Daniel, D., dos Santos, V.B., Vidal, D.T.R., do Lago, C. L., 2015. Determination of biogenic amines in beer and wine by capillary electrophoresis–tandem mass spectrometry. Journal of Chromatography A 1416, 121–128. https://doi.org/10.1016/j.chroma.2015.08.065.

de Aráujo, Álvaro Alberto, Pastore, Gláucia M., Berger, Ralf G., 2002. In: Biotechnology for Fuels and Chemicals. Humana Press, Totowa, NJ, pp. 747–751. https://doi.org/10.1007/978-1-4612-0119-9_60.

De Vuyst, L., Vaningelgem, F., Ghijsels, V., Tsakalidou, E., Leroy, F., 2011. New insights into the citrate metabolism of Enterococcus faecium FAIR-E 198 and its possible impact on the production of fermented dairy products. International dairy journal 21 (9), 580–585. https://doi.org/10.1016/j. idairyj.2011.03.009.

Di Cagno, Raffaella, Surico, Rosalinda F., Paradiso, Annalisa, De Angelis, Maria, Salmon, Jean-Christophe, Buchin, Solange, De Gara, Laura, Gobbetti, Marco, 2009. Effect of autochthonous lactic acid bacteria starters on health-promoting and sensory properties of tomato juices. International journal of food microbiology 128 (3), 473–483. https://doi.org/10.1016/j.ijfoodmicro.2008.10.017.

Diez, A.M., Björkroth, J., Jaime, I., Rovira, J., 2009. Microbial, sensory and volatile changes during the anaerobic cold storage of morcilla de Burgos previously inoculated with Weissella viridescens and Leuconostoc mesenteroides. International Journal of food microbiology 131 (2–3), 168–177. https://doi.org/10.1016/j.ijfoodmicro.2009.02.019.

Dzialo, M.C., Park, R., Steensels, J., Lievens, B., Verstrepen, K.J., 2017. Physiology, ecology and industrial applications of aroma formation in yeast. FEMS Microbiology Reviews 41 (Supp_1), S95–S128. https://doi.org/10.1093/femsre/fux031.

Eng, Thomas, Sasaki, Yusuke, Herbert, Robin A., Lau, Andrew, Trinh, Jessica, Chen, Yan, Mirsiaghi, Mona, Petzold, Christopher J., Mukhopadhyay, Aindrila, 2020. Production of tetra-methylpyrazine using engineered *Corynebacterium glutamicum*. Metabolic Engineering Communications 10, e00115. https://doi.org/10.1016/j.mec.2019.e00115.

Escamilla-Hurtado, M.L., Valdés-Martínez, S.E., Soriano-Santos, J., Gómez-Pliego, R., Verde-Calvo, J.R., Reyes-Dorantes, A., Tomasini-Campocosio, A., 2005. Effect of culture conditions on production of butter flavor compounds by *Pediococcus pentosaceus* and *Lactobacillus acidophilus* in semisolid maize-based cultures. International journal of food microbiology 105 (3), 305–316.

Fadel, H.H., Lotfy, S.N., Asker, M.M., Mahmoud, M.G., Al-Okbi, S.Y., 2018. Nutty-like flavor production by *Corynbacterium glutamicum* 1220T from enzymatic soybean hydrolysate. Effect of encapsulation and storage on the nutty flavoring quality. Journal of Advanced Research 10, 31–38. https://doi.org/10.1016/j.jare.2018.01.003.

Fan, Guangsen, Teng, Chao, Xu, Dai, Fu, Zhilei, Minhazul, Karim A H M, Wu, Qiuhua, Liu, Pengxiao, Yang, Ran, Li, Xiuting, 2019. Enhanced production of ethyl acetate using co-culture of *Wickerhamomyces anomalus* and *Saccharomyces cerevisiae*.

Journal of bioscience and bioengineering 128 (5), 564–570. https://doi.org/10.1016/j.jbiosc.2019.05.002.

Garde, S., Ávila, M., Fernández-García, E., Medina, M., Nuñez, M., 2007. Volatile compounds and aroma of Hispanico cheese manufactured using lacticin 481-producing Lactococcus lactis subsp. lactis INIA 639 as an adjunct culture. International dairy journal 17 (6), 717–726. https://doi.org/10.1016/j.idairyj.2006.07.005.

Guo, Xiangyang, Ho, Chi-Tang, Wan, Xiaochun, Zhu, Hui, Liu, Qiong, Wen, Zhen, 2021. Changes of volatile compounds and odor profiles in Wuyi rock tea during processing. Food Chemistry 341, 128230. https://doi.org/10.1016/j.foodchem.2020.128230.

Hayashi, Yujiro, Yamada, Tomoaki, Sato, Misaki, Watanabe, Shoya, Kwon, Eunsang, Iwasaki, Kotaro, Umemiya, Shigenobu, 2019. Asymmetric Michael Reaction of α-CF3 Thioester and α, β-Unsaturated Aldehyde Catalyzed by Diphenylprolinol Silyl Ether. Organic letters 21 (13), 5183–5186. https://doi.org/10.1021/acs.orglett.9b0177410.1021/acs.orglett.9b01774.s001.

Ianni, A., Bennato, F., Martino, C., Grotta, L., Martino, G., 2020. Volatile flavor compounds in cheese as affected by ruminant diet. Molecules 25 (3), 461. https://doi.org/10.3390/molecules25030461.

Inui, H., Ishikawa, T., Tamoi, M., 2017. Wax ester fermentation and its application for biofuel production. In *Euglena: biochemistry, cell and molecular biology*. Springer, Cham, pp. 269–283.

Janssens, T.K., Tyc, O., Besselink, H., de Boer, W., Garbeva, P., 2019. Biological activities associated with the volatile compound 2, 5-bis (1-methylethyl)-pyrazine. FEMS microbiology letters 366 (3), fnz023. https://doi.org/10.1093/femsle/fnz023.

Kendirci, P., Salum, P., Bas, D., Erbay, Z., 2020. Production of enzyme-modified cheese (EMC) with ripened white cheese flavour: II-Effects of lipases. Food and Bioproducts Processing 122, 230–244. https://doi.org/10.1016/j.fbp.2020.05.010.

Khan, R.A.A., Najeeb, S., Hussain, S., Xie, B., Li, Y., 2020. Bioactive Secondary Metabolites from *Trichoderma* spp. against Phytopathogenic Fungi. *Microorganisms* 8 (6), 817. https://doi.org/10.3390/microorganisms8060817.

Kim, T.Y., Lee, S.W., Oh, M.K., 2014. Biosynthesis of 2-phenylethanol from glucose with genetically engineered *Kluyveromyces marxianus*. Enzyme and Microbial Technology 61, 44–47. https://doi.org/10.1016/j.enzmictec.2014.04.011.

Lew, L.C., Liong, M.T., 2013. Bioactives from probiotics for dermal health: functions and benefits. Journal of applied microbiology 114 (5), 1241–1253. https://doi.org/10.1111/jam.12137.

Li, T., Sun, X., Chen, H., He, B., Mei, Y., Wang, D., Li, J., 2020a. Effect of the Combination of Vanillin and Chitosan Coating on the Microbial Diversity and Shelf-Life of Refrigerated Turbot (*Scophthalmus maximus*) Filets. Frontiers in Microbiology 11, 462. https://doi.org/10.3389/fmicb.2020.00462.

Li, Xiaolu, Feng, Qian, Qu, Lejing, Zhao, Ting, Li, Xiaoan, Bai, Tiantian, Sun, Shisheng, Wu, Shaoping, Zhang, Yongmin, Li, Jianli, 2020b. A water-soluble and incubate-free fluorescent environment-sensitive probe for ultrafast visualization of protein thiols within living cells. Analytica Chimica Acta 1126, 72–81. https://doi.org/10.1016/j.aca.2020.06.026.

Liang, Caice, Ding, Sai, Sun, Wenjun, Liu, Li, Zhao, Wei, Zhang, Deli, Ying, Hanjie, Liu, Dong, Chen, Yong, 2020. Biofilm-based fermentation: a novel immobilisation strategy for *Saccharomyces cerevisiae* cell cycle progression during ethanol production. Applied Microbiology and BiotechnoloLianggy 104 (17), 7495–7505. https://doi.org/10.1007/s00253-020-10770-1.

Marella, Eko Roy, Dahlin, Jonathan, Dam, Marie Inger, ter Horst, Jolanda, Christensen, Hanne Bjerre, Sudarsan, Suresh, Wang, Guokun, Holkenbrink, Carina, Borodina, Irina, 2020. A single-host fermentation process for the production of flavor lactones from non-hydroxylated fatty acids. Metabolic engineering 61, 427–436. https://doi.org/10.1016/j.ymben.2019.08.009.

Marti-Quijal, F.J., Remize, F., Meca, G., Ferrer, E., Ruiz, M.J., Barba, F.J., 2020. Fermentation in fish and by-products processing: An overview of current research and future prospects. Current Opinion in Food Science 31, 9–16. https://doi.org/10.1016/j.cofs.2019.08.001.

Marui, J., Boulom, S., Panthavee, W., Momma, M., Kusumoto, K. I., Nakahara, K., & Saito, M. (2014). Culture-independent analysis of the bacterial community during fermentation of pa-som, a traditional fermented fish product in Laos. Fisheries science, 80(5), 1109-1115. https://doi.org/10.1007/s12562-014-0780-4

Merveille, T.O., Denis, Z., Abdel, N.J., Ursula, A.A., Adie, A.F.A.M., Smith, B.B., Clement, A.N.J., 2017. Antimicrobial Activities of Some Medicinal Plants against Multiresistants Microorganisms Causing Urogenital Tract Infections in Cameroon. Journal of Diseases and Medicinal Plants 3 (2), 33–41.

Misihairabgwi, J., Cheikhyoussef, A., 2017. Traditional fermented foods and beverages of Namibia. Journal of Ethnic Foods 4 (3), 145–153. https://doi.org/10.1016/j.jef.2017.08.001.

Montanari, Chiara, Gatto, Veronica, Torriani, Sandra, Barbieri, Federica, Bargossi, Eleonora, Lanciotti, Rosalba, Grazia, Luigi, Magnani, Rudy, Tabanelli, Giulia, Gardini, Fausto, 2018. Effects of the diameter on physico-chemical, microbiological and volatile profile in dry fermented sausages produced with two different starter cultures. Food Bioscience 22, 9–18. https://doi.org/10.1016/j.fbio.2017.12.013.

Mortzfeld, Frederik B., Hashem, Chiam, Vranková, Kvetoslava, Winkler, Margit, Rudroff, Florian, 2020. Pyrazines: Synthesis and Industrial Application of these Valuable Flavor and Fragrance Compounds. Biotechnology Journal 15 (11), 2000064. https://doi.org/10.1002/biot.v15.1110.1002/biot.202000064.

October, F.M., 2020. *Effect of yeasts and oenological parameters on acetaldehyde production during alcoholic fermentation of South African grape musts* (Doctoral dissertation. Stellenbosch University), Stellenbosch.

Omar, K.A., Gounga, M.E., Liu, R., Mlyuka, E., Wang, X., 2016. Effects of microbial lipases on hydrolyzed milk fat at different time intervals in flavour development and oxidative stability. Journal of food science and technology 53 (2), 1035–1046. https://doi.org/10.1007/s13197-015-2158-8.

Otto, Maike, Wynands, Benedikt, Marienhagen, Jan, Blank, Lars M., Wierckx, Nick, 2020. Benzoate synthesis from glucose or glycerol using engineered *Pseudomonas taiwanensis*. Biotechnology Journal 15 (11), 2000211. https://doi.org/10.1002/biot.v15.1110.1002/biot.202000211.

Patel, A., Shah, N., 2014. Current scenario in antimicrobial compounds produced by food grade bacteria in relation to enhance food safety and quality. Journal of Innovative Biology 1 (4), 189–194.

Patel, A., Shah, N., Prajapati, J.B., 2013. Biosynthesis of vitamins and enzymes in fermented foods by lactic acid bacteria and related genera - a promising approach. Croatian Journal of Food Science & Technology 5 (2), 85–91.

Paterson, A., & Piggott, J. R. (2006). Flavour in sourdough breads: a review. Trends in Food Science & Technology, 17(10), 557-566. Doi: 10.1016/j.tifs.2006.03.006.

Paulino, B.N., Sales, A., de Oliveira Felipe, L., Pastore, G.M., Molina, G., Bicas, J.L., 2021. Recent advances in the microbial and enzymatic production of aroma compounds. Current Opinion in Food Science. 37, 98–106. https://doi.org/10.1016/j.cofs.2020.09.010.

Perea-Sanz, Laura, López-Díez, José Javier, Belloch, Carmela, Flores, Mónica, 2020. Counteracting the effect of reducing nitrate/nitrite levels on dry fermented sausage aroma by *Debaryomyces hansenii* inoculation. Meat Science 164, 108103. https://doi.org/10.1016/j.meatsci.2020.108103.

Perea-Sanz, L., Montero, R., Belloch, C., Flores, M., 2019. Microbial changes and aroma profile of nitrate reduced dry sausages during vacuum storage. Meat Science 147, 100–107. https://doi.org/10.1016/j.meatsci.2018.08.026.

Petrovici, Anca Roxana, Ciolacu, Diana Elena, 2018. In: Generation of Aromas and Flavours. InTech. https://doi.org/10.5772/intechopen.76785.

Prabakaran, Rajalakshmi, Marie, J. Margaret, Xavier, A. John Maria, 2020. Biobased Unsaturated Polyesters Containing Castor Oil-Derived Ricinoleic Acid and Itaconic Acid: Synthesis, In Vitro Antibacterial, and Cytocompatibility Studies. ACS Applied Bio Materials 3 (9), 5708–5721. https://doi.org/10.1021/acsabm.0c0048010.1021/acsabm.0c00480.s001.

Reale, Anna, Ianniello, Rocco G., Ciocia, Felicia, Di Renzo, Tiziana, Boscaino, Floriana, Ricciardi, Annamaria, Coppola, Raffaele, Parente, Eugenio, Zotta, Teresa, McSweeney, Paul L.H., 2016. Effect of respirative and catalase-positive Lactobacillus casei adjuncts on the production and quality of Cheddar-type cheese. International Dairy Journal 63, 78–87. https://doi.org/10.1016/j.idairyj.2016.08.005.

Rivas-Cañedo, A., Juez-Ojeda, C., Nuñez, M., Fernández-García, E., 2011. Effects of high-pressure processing on the volatile compounds of sliced cooked pork shoulder during refrigerated storage. Food chemistry 124 (3), 749–758. https://doi.org/10.1016/j.foodchem.2010.06.091.

Roman, S., Sánchez-Siles, L.M., Siegrist, M., 2017. The importance of food naturalness for consumers: Results of a systematic review. Trends in food science & technology 67, 44–57. https://doi.org/10.1016/j.tifs.2017.06.010.

Rosca, I., Petrovici, A.R., Brebu, M., Stoica, I., Minea, B., Marangoci, N., 2016. An original method for producing acetaldehyde and diacetyl by yeast fermentation. brazilian journal of microbiology 47, 949–954. https://doi.org/10.1016/j.bjm.2016.07.005.

Sarıcaoglu, Furkan Turker, Turhan, Sadettin, 2020. Physicochemical, antioxidant and antimicrobial properties of mechanically deboned chicken meat protein films enriched with various essential oils. Food Packaging and Shelf Life 25, 100527. https://doi.org/10.1016/j.fpsl.2020.100527.

Serio, A., Chaves-López, C., Paparella, A., Suzzi, G., 2010. Evaluation of metabolic activities of enterococci isolated from Pecorino Abruzzese cheese. International Dairy Journal 20 (7), 459–464. https://doi.org/10.1016/j.idairyj.2010.02.005.

Sharma, A., Sharma, P., Singh, J., Singh, S., Nain, L., 2020a. Prospecting the Potential of Agroresidues as Substrate for Microbial Flavor Production. Frontiers in Sustainable Food Systems 4, 18. https://doi.org/10.3389/fsufs.2020.00018.

Sharma, R., Garg, P., Kumar, P., Bhatia, S.K., Kulshrestha, S., 2020b. Microbial fermentation and its role in quality improvement of fermented foods. Fermentation 6 (4), 106.

Siddiquee, Shafiquzzaman, 2017. In: Volatiles and Food Security. Springer Singapore, Singapore, pp. 313–333. https://doi.org/10.1007/978-981-10-5553-9_17.

Sidira, M., Kandylis, P., Kanellaki, M., Kourkoutas, Y., 2016. Effect of curing salts and probiotic cultures on the evolution of flavor compounds in dry-fermented sausages during ripening. Food Chemistry 201, 334–338. https://doi.org/10.1016/j.foodchem.2016.01.084.

Silva, R., Pereira, J., Rouxinol, M., Patarata, L., 2020. Sensory Changes and *Listeria monocytogenes* Behavior in Sliced Cured Pork Loins during Extended Storage. Foods 9 (5), 621. https://doi.org/10.3390/foods9050621.

Siragusa, S., Fontana, C., Cappa, F., Caputo, L., Cocconcelli, P.S., Gobbetti, M., De Angelis, M., 2011. Disruption of the gene encoding glutamate dehydrogenase affects growth, amino acids catabolism and survival of *Lactobacillus plantarum* UC1001. International dairy journal 21 (2), 59–68. https://doi.org/10.1016/j.idairyj.2010.09.001.

Suwannakham, Supaporn, Yang, Shang-Tian, 2005. Enhanced propionic acid fermentation by Propionibacterium acidipropionici mutant obtained by adaptation in a fibrous-bed bioreactor. Biotechnology and bioengineering 91 (3), 325–337.

Suwannakham, Supaporn, Huang, Yan, Yang, Shang-Tian, 2006. Construction and characterization of ack knock-out mutants of Propionibacterium acidipropionici for enhanced propionic acid fermentation. Biotechnology and bioengineering 94 (2), 383–395.

Tang, P.L., Hassan, O., 2020. Bioconversion of ferulic acid attained from pineapple peels and pineapple crown leaves into vanillic acid and vanillin by *Aspergillus niger* I-1472. BMC chemistry 14 (1), 7. https://doi.org/10.1186/s13065-020-0663-y.

Thierry, Anne, Collins, Yvonne F., Abeijón Mukdsi, M.C., McSweeney, Paul L.H., Wilkinson, Martin G., Spinnler, Henri E., 2017. In: Cheese. Elsevier, pp. 423–444. https://doi.org/10.1016/B978-0-12-417012-4.00017-X.

Tometri, Sara Shokri, Ahmady, Mohammad, Ariaii, Peiman, Soltani, Mahdi Sharifi, 2020. Extraction and encapsulation of *Laurus nobilis* leaf extract with nano-liposome and its effect on oxidative, microbial, bacterial and sensory properties of minced beef. Journal of Food Measurement and Characterization 14 (6), 3333–3344. https://doi.org/10.1007/s11694-020-00578-y.

Try, S., Voilley, A., Chunhieng, T., De-Coninck, J., Waché, Y., 2018. Aroma compounds production by solid state fermentation, importance of in situ gas-phase recovery systems. Applied Microbiology and Biotechnology 102 (17), 7239–7255. https://doi.org/10.1007/s00253-018-9157-4.

Ullah, Ihsan, Khan, Abdul Latif, Ali, Liaqat, Khan, Abdur Rahim, Waqas, Muhammad, Hussain, Javid, Lee, In-Jung, Shin, Jae-Ho, 2015. Benzaldehyde as an insecticidal, antimicrobial, and antioxidant compound produced by *Photorhabdus temperata* M1021. Journal of Microbiology 53 (2), 127–133. https://doi.org/10.1007/s12275-015-4632-4.

van Kranenburg, Richard, Kleerebezem, Michiel, van Hylckama Vlieg, Johan, Ursing, Björn M, Boekhorst, Jos, Smit, Bart A, Ayad, Eman H.E, Smit, Gerrit, Siezen, Roland J, 2002. Flavour formation from amino acids by lactic acid bacteria: predictions from genome sequence analysis. International Dairy Journal 12 (2-3), 111–121. https://doi.org/10.1016/S0958-6946(01)00132-7.

Vandamme, Erick J, Soetaert, Wim, 2002. Bioflavours and fragrances via fermentation and biocatalysis. Journal of Chemical Technology & Biotechnology: International Research in Process, Environmental & Clean Technology 77 (12), 1323–1332. https://doi.org/10.1002/(ISSN)1097-466010.1002/jctb.v77:1210.1002/jctb.722.

Walsh, A.M., Crispie, F., Kilcawley, K., O'Sullivan, O., O'Sullivan, M.G., Claesson, M.J., Cotter, P.D., 2016. Microbial succession and flavor production in the fermented dairy beverage kefir. Msystems 1 (5), e00052–e116. https://doi.org/10.1128/mSystems.00052-16.

Wang, Diqiang, Chen, Liangqiang, Yang, Fan, Wang, Heyu, Wang, Li, 2019a. Yeasts and their importance to the flavour of traditional Chinese liquor: a review. Journal of the Institute of Brewing 125 (2), 214–221. https://doi.org/10.1002/jib.v125.210.1002/jib.552.

Wang, L., Ying, Y., Hu, Z., Wang, T., Shen, X., Wu, P., 2016. Simultaneous determination of 2-and 3-MCPD esters in infant formula milk powder by solid-phase extraction and GC-MS analysis. Journal of AOAC International 99 (3), 786–791. https://doi.org/10.5740/jaoacint.15-0310.

Wang, S., Chen, P., Dang, H., 2019b. Lactic Acid Bacteria and γ-Aminobutyric Acid and Diacetyl. In: Lactic Acid Bacteria. Springer, Singapore, pp. 1–19.

Wang, W., Xia, W., Gao, P., Xu, Y., Jiang, Q., 2017. Proteolysis during fermentation of Suanyu as a traditional fermented fish product of China. International Journal of Food Properties 20 (sup1), S166–S176. https://doi.org/10.1080/10942912.2017.1293089.

Wang, Yaqin, Trani, Antonio, Knaapila, Antti, Hietala, Sami, Coda, Rossana, Katina, Kati, Maina, Ndegwa Henry, 2020a. The effect of in situ produced dextran on flavour and texture perception of wholegrain sorghum bread. Food Hydrocolloids 106, 105913. https://doi.org/10.1016/j.foodhyd.2020.105913.

Wang, Zehan, Xu, Zhe, Sun, Liming, Dong, Liang, Wang, Zhenyu, Du, Ming, 2020b. Dynamics of microbial communities, texture and flavor in Suan zuo yu during fermentation. Food Chemistry 332, 127364. https://doi.org/10.1016/j.foodchem.2020.127364.

Williams-Campbell, A.M., Jay, J.M., 2002. Effects of diacetyl and carbon dioxide on spoilage microflora in ground beef. Journal of food protection 65 (3), 523–527.

Xia, J., Yang, Y., Liu, C.G., Yang, S., Bai, F.W., 2019. Engineering *Zymomonas mobilis* for robust cellulosic ethanol production. Trends in Biotechnology 37 (9), 960–972. https://doi.org/10.1016/j.tibtech.2019.02.002.

Xu, Y., Minhazul, K. A., & Li, X. (2020). The occurrence, enzymatic production, and application of ethyl butanoate, an important flavor constituent. *Flavour and Fragrance Journal*, *35*(6), 601-615. https://doi.org/10.1002/ffj.3613

Yang, Zhaoxia, Liu, Sasa, Lv, Jing, Sun, Zeping, Xu, Wenhuan, Ji, Chaofan, Liang, Huipeng, Li, Shengjie, Yu, Chenxu, Lin, Xinping, 2020. Microbial succession and the changes of flavor and aroma in *Chouguiyu*, a traditional Chinese fermented fish. Food Bioscience 37, 100725. https://doi.org/10.1016/j.fbio.2020.100725.

Zakaria, S.M., Kamal, S.M.M., 2016. Subcritical water extraction of bioactive compounds from plants and algae: applications in pharmaceutical and food ingredients. Food Engineering Reviews 8 (1), 23–34. https://doi.org/10.1007/s12393-015-9119-x.

Zhang, Huaizhi, Zhang, Lijie, Yu, Xiaowei, Xu, Yan, 2020a. The biosynthesis mechanism involving 2, 3-pentanedione and aminoacetone describes the production of 2-Ethyl-3, 5-dimethylpyrazine and 2-Ethyl-3, 6-dimethylpyrazine by *Bacillus subtilis*. Journal of Agricultural and Food Chemistry 68 (11), 3558–3567. https://doi.org/10.1021/acs.jafc.9b0780910.1021/acs.jafc.9b07809.s001.

Zhang, L., Cao, Y., Tong, J., Xu, Y., 2019. An alkylpyrazine synthesis mechanism involving L-threonine-3-dehydrogenase describes the production of 2, 5-dimethylpyrazine and 2, 3, 5-trimethylpyrazine by *Bacillus subtilis*. Applied and Environmental Microbiology 85 (24), e01807–e1819. https://doi.org/10.1128/AEM.01807-19.

Zhang, Shangjie, Guo, Feng, Yan, Wei, Dong, Weiliang, Zhou, Jie, Zhang, Wenming, Xin, Fengxue, Jiang, Min, 2020b. Perspectives for the microbial production of ethyl acetate. Applied Microbiology and Biotechnology 104 (17), 7239–7245. https://doi.org/10.1007/s00253-020-10756-z.

Zheng, Xiaochun, Ge, Zhengkai, Lin, Ke, Zhang, Dandan, Chen, Yu, Xiao, Jing, Wang, Bin, Shi, Xuewei, 2021. Dynamic changes in bacterial microbiota succession and flavour development during milk fermentation of Kazak artisanal cheese. International Dairy Journal 113, 104878. https://doi.org/10.1016/j.idairyj.2020.104878.

Zinjanab, M.S., Golmakani, M.T., Eskandari, M.H., Toh, M., Liu, S.Q., 2021. Natural flavor biosynthesis by lipase in fermented milk using in situ produced ethanol. Journal of Food Science and Technology 58 (5), 1858–1868. https://doi.org/10.1007/s13197-020-04697-8.

Zuljan, F.A., Mortera, P., Alarcón, S.H., Blancato, V.S., Espariz, M., Magni, C., 2016. Lactic acid bacteria decarboxylation reactions in cheese. International Dairy Journal 62, 53–62. https://doi.org/10.1016/j.idairyj.2016.07.007.