Review

Formation and Characterization of Aroma Compounds in Camembert Cheese

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Formation and Characterization of Aroma Compounds in Camembert Cheese

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Abstract: The characterization of volatile compounds in cheese is crucial for understanding sensory properties and consumer acceptance. Camembert cheese, a surface-ripened variety, presents a complex aroma profile shaped by biochemical and microbial interactions. Despite advances in analytical methods such as gas chromatography-mass spectrometry (GC-MS) and gas chromatography-olfactometry (GC-O), the metabolic pathways and microbial interactions defining Camembert's aroma remain incompletely understood. This review explores the synergistic roles of microbial communities, enzymatic activity, and environmental conditions in volatile compound formation. A systematic literature review was conducted using Scopus, Web of Science, and Google Scholar to analyze the classification of volatile compounds, biochemical pathways of aroma formation, and microbial contributions. The findings highlight the essential role of *Penicillium camemberti* and lactic acid bacteria in aroma modulation, particularly in sulfur compounds, esters, and short-chain fatty acids. Emerging technologies such as solid-phase microextraction (SPME) and metabolomics provide new insights into volatile compound dynamics. Understanding these mechanisms may enhance aroma control in cheese production through microbial engineering and biochemical monitoring. This review underscores the need for integrated approaches to optimize fermentation and ensure sensory standardization, contributing to improved quality and consumer acceptance of Camembert cheese.

Keywords: Volatile compounds; Camembert cheese; Aroma formation; Microbial metabolism

1. Introduction

Volatile compounds are essential in shaping the flavor profile of cheeses, directly influencing their sensory perception and commercial acceptance. Most of these compounds result from complex biochemical processes that occur during ripening, involving reactions such as proteolysis, lipolysis, and microbial metabolism [1]. In the case of white mold-ripened cheeses, such as Brie and Camembert, the aroma profile is particularly diverse, being modulated by the activity of specific microorganisms, such as *Penicillium camemberti* and *Lactococcus lactis*, which contribute resulting in the production of acids, esters, ketones, and alcohols responsible for characteristic notes of mushroom, butter, and ammonia [2,3].

Despite significant advances in the characterization of these compounds, gaps remain in understanding the chemical and metabolic interactions that determine the final aroma of Camembert [4]. Additionally, environmental, technological, and microbiological factors directly influence the volatile composition of the cheese, potentially affecting its sensory acceptance and overall quality [5]. While some studies suggest that modifications in the ripening process can be explored to optimize the aroma profile, the variability in volatile compound formation is still not fully understood.

Given this context, this review aims to explore the complexity of Camembert cheese aroma by identifying the main classes of volatile compounds and their respective biochemical formation pathways. Furthermore, this review seeks to analyze the microbiological interactions during ripening and discuss the practical implications of these findings within the dairy sector, offering a thorough analysis of the factors that influence the sensory quality of this cheese.

2. Materials and Methods

This study is based on a literature review aimed at identifying and analyzing the volatile compounds responsible for the characteristic aroma of Camembert cheese, as well as the biochemical and microbiological mechanisms involved in its formation. The search for publications was conducted in the Scopus, Web of Science, and Google Scholar databases using keywords such as “volatile compounds”, “aroma”, “Camembert cheese”, “gas chromatography (GC)”, and “solid-phase microextraction (SPME)”. These terms were selected to encompass relevant studies on Camembert’s odor-active volatile profile, the associated biochemical processes, and the analytical techniques used to characterize these compounds.

The selection criteria for articles were based on their relevance to the review’s scope, including: (i) studies addressing the volatile and odor-active composition of Camembert; (ii) articles describing the biochemical and microbiological processes associated with the formation of volatile and odor-active compounds; and (iii) publications utilizing analytical techniques such as gas chromatography (GC), mass spectrometry (MS), and solid-phase microextraction (SPME), in addition to olfactometric techniques like gas chromatography-olfactometry (GC-O), when available. Although the primary focus was Camembert, studies on other white mold cheeses, such as Brie, were included when they provided directly relevant insights for the review. There was no temporal restriction, as the selection prioritized studies that made significant contributions to the topic. Publications focusing exclusively on other cheese types, such as washed-rind cheeses (e.g., Munster, Taleggio), blue cheeses, or pressed cheeses (e.g., Gouda, Cheddar), were excluded.

Advanced techniques, such as Aroma Extract Dilution Analysis (AEDA) and Odor Activity Value (OAV) determination, although widely recognized in aroma studies of fermented foods, have been systematically applied to white mold cheeses to a lesser extent. Therefore, their relevance and potential future applications are discussed in detail throughout this review.

The collected data were organized into three main analytical categories: (i) classification of volatile compounds, grouping substances like alcohols, fatty acids, esters, and sulfur compounds; (ii) general biochemical pathways of volatile compound formation, with an emphasis on lipolysis, proteolysis, and carbohydrate metabolism; and (iii) microbial contributions, highlighting the role of microorganisms such as *Penicillium camemberti* and lactic acid bacteria in shaping Camembert’s aroma profile.

3. Results

3.1. Odor-Active Volatile Profile of Camembert Cheese

Camembert cheese is characterized by a complex and diverse volatile profile, resulting from the interaction of biochemical, microbiological, and physical processes throughout ripening. This sensory richness stems from the occurrence of volatile compounds primarily formed through proteolysis, lipolysis, and microbial metabolism [1].

Microorganisms such as *Penicillium camemberti* and *Lactococcus lactis* play essential roles in generating these compounds, imparting fruity, buttery, pungent, and slightly ammoniacal notes to the cheese [3]. Additionally, environmental factors such as temperature, humidity, and salinity directly influence the volatile composition of the cheese, impacting its final sensory perception [6].

The aroma of Camembert arises from the presence and interaction of various classes of odor-active volatile compounds, predominantly lipophilic, formed through enzymatic and chemical reactions involving free fatty acids, peptides, amino acids, and carbohydrates [7]. During ripening, these compounds may undergo secondary transformations, including reduction, oxidation, and chemical interactions, forming more stable structures [3].

Nevertheless, the impact of odor-active volatile compounds on the aroma varies. Their influence depends on factors such as concentration, olfactory perception threshold, and synergistic interactions within the cheese matrix [4]. Table 1 presents the main odor-active volatile compounds identified in Camembert and their associated sensory characteristics.

Table 1. Odor-Active Volatile Compounds Associated with Camembert (Adapted from [4,8–13]).

Compound	Aroma Notes
Methanethiol	Cooked cabbage, sulfur
Ethanol	Alcoholic, mild
Acetone	Ethereal, fruity
Dimethyl sulfide	Boiled cabbage, sulfur
Acetic acid	Vinegar, pungent
Propionic acid	Vinegar, pungent
2-Pentanone	Fruity, sweet
Dimethyl disulfide	Cauliflower, garlic
Butanoic acid	Rancid, cheesy, sweaty
2-Heptanone	Blue cheese, spicy
Propanol	Alcoholic, sweet
2,3-Butanedione	Buttery
Ethyl acetate	Solvent, pineapple, fruity
Methyl thioacetate	Cooked cauliflower
3-Methylbutanol	Fruity, alcohol-like
3-Methylbutanal	Green, malty
2-Nonanone	Sweet, soapy, floral
Hexanoic acid	Rancid, sweaty, sour
Octanoic acid	Goaty, waxy, rancid
γ-Hexalactone	Caramel, nutty, woody
Benzeneacetaldehyde	Floral, sweet, fruity
3-Methylbutanoic acid	Rancid, sweaty, pungent

Although Table 1 presents a broad range of odor-active volatile compounds identified in Camembert cheese, not all of them contribute equally to its sensory perception. The aromatic relevance of each compound depends on factors such as its concentration, perception threshold, and interactions within the cheese matrix. Analytical–sensory techniques, including gas chromatography–olfactometry (GC-O) and solid-phase microextraction combined with mass spectrometry (SPME-GC–MS), have been employed to characterize these compounds in surface-ripened cheeses, although their application to Camembert remains relatively limited and fragmented [7–9,12]. Among the identified compounds, methanethiol, dimethyl disulfide, 2,3-butanedione, ethyl acetate, and 3-methylbutanoic acid stand out due to their low detection thresholds and intense sensory attributes [7,8,12]. Addressing the current gap through more systematic use of omission tests or odor activity value (OAV) analysis could further refine our understanding of which compounds truly shape Camembert's distinctive aroma.

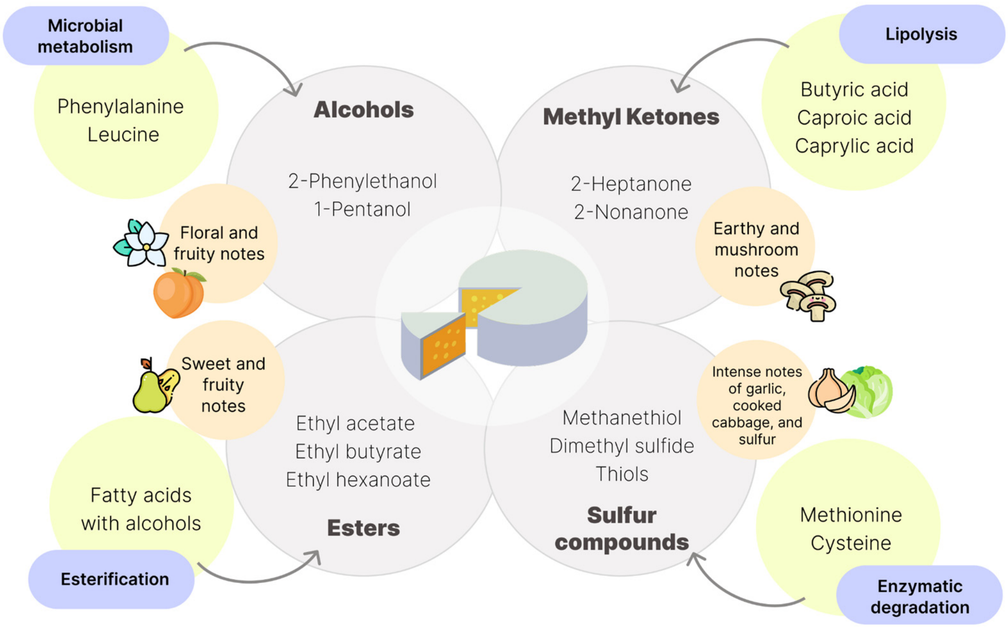

Figure 1. Key biochemical pathways contributing to the aroma development of Camembert cheese. Some icons used in this figure were sourced from Flaticon.com and are used in accordance with their free license with attribution.

3.2. Biochemical Origin of Odor-Active Volatile Compounds in Camembert Cheese

The sensory perception of ripened cheeses is directly related to their chemical composition, with volatile compounds being the primary contributors to their characteristic aroma. In the case of Camembert, these compounds are generated through a series of interconnected biochemical processes throughout production and ripening, including lipolysis, proteolysis, and carbohydrate metabolism [14].

As illustrated in Table 2, three main metabolic pathways influence the formation of volatile compounds responsible for the aroma of Camembert [15]:

Table 2. Metabolic pathways for the formation of volatile compounds in Camembert cheese.

Process	Description	Formed Compounds	Sensory Contribution
Lactose Catabolism	Degradation of lactose generating organic acids, diacetyl, and volatile aroma precursor compounds.	Organic acids, diacetyl, volatile compounds	Acidic, buttery, mildly pungent notes
Lipolysis	Breakdown of lipids into free fatty acids, which can be converted into ketones, esters, and lactones.	Ketones, esters, lactones	Fruity, buttery, pungent notes
Proteolysis	Hydrolysis of proteins into peptides and amino acids, serving as substrates for sulfur compounds, higher alcohols, and aldehydes.	Sulfur compounds, higher alcohols, aldehydes	Sulfurous, nutty notes

The quality of raw milk, along with fermentation and ripening conditions, plays a decisive role in shaping the aroma profile of Camembert. The composition of the present microorganisms directly influences the production of fatty acids, alcohols, esters, ketones, and lactones—compounds that define the cheese's sensory nuances [16].

Ripening is the primary factor that determines the final flavor, as it involves a series of biochemical reactions that can be categorized into two major groups: primary and secondary metabolism, as illustrated in Figure 2.

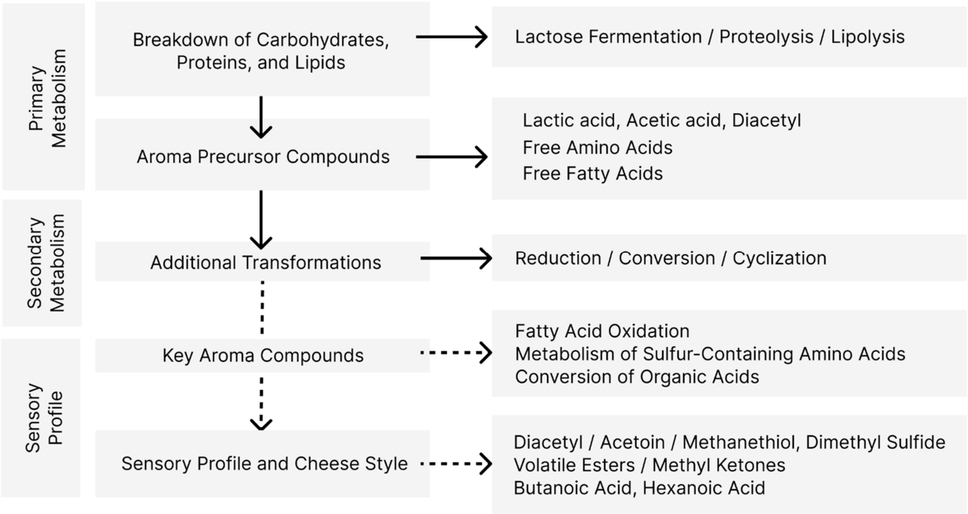

Figure 2. Stages of aroma compound formation in cheese (Adapted from [17–20]). The diagram is divided into three stages: Primary Metabolism and Secondary Metabolism, which represent the sequential formation of aroma precursors and their transformation into key volatile compounds; and Sensory Profile, which illustrates how these compounds contribute to the final perceptible aroma of cheeses like Camembert. Some compounds, such as diacetyl and butanoic acid, may appear in multiple stages due to their dual role as intermediates and final odor-active compounds.

In addition to lactic acid bacteria, yeasts present during ripening play a crucial role by producing secondary metabolites such as carbonyl compounds, sulfur compounds, fatty acids, and higher alcohols, which enhance the aroma and flavor of Camembert [21]. Additionally, the fungus *Penicillium camemberti* plays a central role in the ripening of this cheese, promoting the development of its characteristic white rind and actively contributing to its sensory profile. This fungus produces proteolytic and lipolytic enzymes that degrade proteins and lipids, generating precursors of volatile compounds responsible for specific aroma notes [7,30].

Mushroom-like notes are associated with the presence of 1-octen-3-ol and methanethiol, while the buttery aroma is predominantly influenced by 2,3-butanedione (diacetyl) and acetoin. Meanwhile, ammoniacal nuances result from ammonia (NH_3) release and the metabolism of sulfur-containing amino acids, leading to the formation of compounds such as dimethyl sulfide, trimethylamine, and methanethiol, which play a fundamental role in defining Camembert's sensory profile [12]. The synergistic interaction between lactic acid bacteria, yeasts, and *Penicillium camemberti* results in a matrix rich in volatile compounds, whose complexity defines the unique aroma and flavor of Camembert [4,7–13]. The following sections will detail the general biochemical pathways involved in the formation of odor-active volatile compounds found in white mold-ripened cheeses.

3.2.1. Carbohydrate Metabolism and the Formation of Aroma Compounds

The degradation of carbohydrates plays a crucial role in the formation of volatile compounds in Camembert cheese. During the early stages of ripening, lactose is fermented by lactic acid bacteria (LAB), such as *Lactococcus lactis* and *Leuconostoc mesenteroides*, leading to the production of lactic acid, which contributes to the cheese's acidity and texture [16,18].

Following this initial metabolism, secondary transformations occur, involving the conversion of lactic acid into compounds such as acetic acid, propionic acid, ethanol, and diacetyl, which play an essential role in the aroma complexity of the cheese. These processes and their microbial interactions are detailed in Figure 3, which illustrates the formation of volatile compounds derived from carbohydrate metabolism throughout the ripening of Camembert.

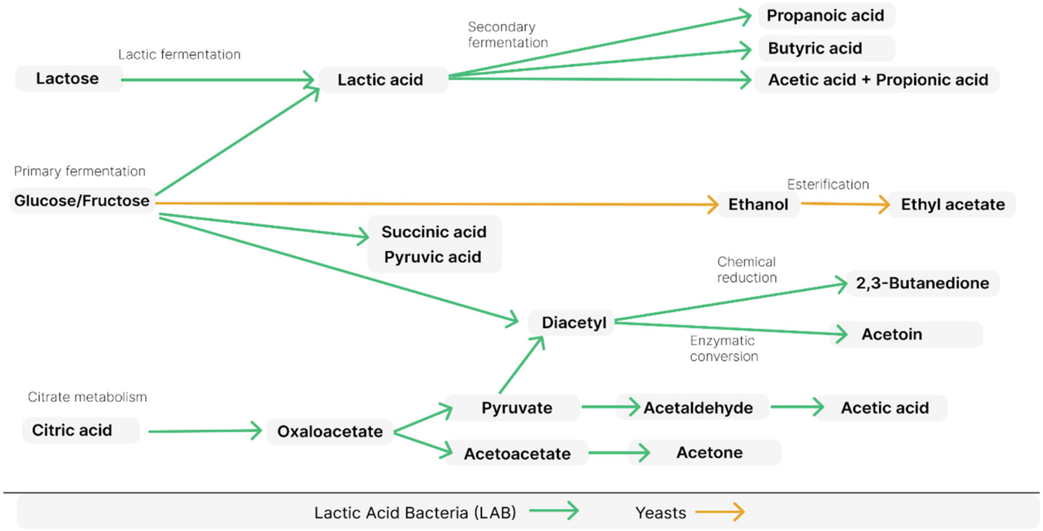

Figure 3. Pathways of aroma compound formation from carbohydrate metabolism (Adapted from [15]).

During ripening, lactic acid bacteria such as *Lactococcus lactis* and *Geotrichum candidum* metabolize milk lactose, generating glucose and other intermediates that can serve as substrates for secondary reactions. These processes lead to the formation of metabolites such as ethanol, which, in turn, acts as a precursor for volatile esters, including ethyl acetate and methyl butyrate, responsible for mild alcoholic and fruity notes [22].

Lactose is the primary carbohydrate in milk and can vary by up to 100 g/L among different mammalian species [16]. Its metabolism results in the production of compounds such as L-lactate and DL-lactate, which directly influence the flavor of ripened cheeses, including Camembert, Cheddar, and Dutch cheeses. L-lactate contributes to a slight acidity and freshness in flavor, while DL-lactate, depending on its concentration, can affect the perception of creaminess and aroma complexity. Consequently, these compounds serve as substrates for secondary reactions that lead to the formation of organic acids, such as acetic and propionic acid, responsible for mildly pungent and fruity notes in ripened cheeses [23].

Leuconostoc spp., a genus of lactic acid bacteria involved in Camembert ripening, plays an important role in the production of aroma compounds by metabolizing citrate, leading to the formation of diacetyl and acetate, which contribute buttery notes and complexity to the aroma. Additionally, its metabolic activity may contribute to ethanol and organic acid production, further enhancing the cheese's sensory diversity [24].

Citrate, present in milk at concentrations of up to 1.8 g/L, is often lost in the whey during processing but significantly impacts the sensory profile of certain cheeses. Mesophilic bacteria, such as *Lactococcus lactis* and *Leuconostoc spp*., metabolize citrate to produce compounds such as acetate, diacetyl, acetoin, and CO_2, which contribute to the aroma of cheeses like Quark, Cottage, and Dutch cheeses [25]. The main compounds resulting from citrate metabolism play fundamental roles in cheese sensory characteristics. Diacetyl is a key compound responsible for pronounced buttery notes, especially in intensely flavored cheeses. Carbon dioxide (CO_2) contributes to the formation of "eyes" in cheeses like Gouda, influencing their texture. Meanwhile, acetate and acetoin add slightly acidic characteristics, modulating flavor balance and enhancing aroma complexity. However, excessive citrate metabolism can affect cheese texture. In varieties such as Cheddar, its intense degradation can lead to structural softening, compromising the final product's integrity [26].

3.2.2. Odor-Active Volatiles Formed by Fatty Acid Metabolism

Lipolysis is one of the most important biochemical processes in the ripening of Camembert cheese, playing a central role in the development of its aroma, flavor, and texture. This process, which is best illustrated in Figure 4, involves the hydrolysis of triglycerides present in milk fat, releasing free fatty acids (FFA) that serve as precursors for a wide range of volatile compounds, including esters, lactones, alcohols, and ketones [25].

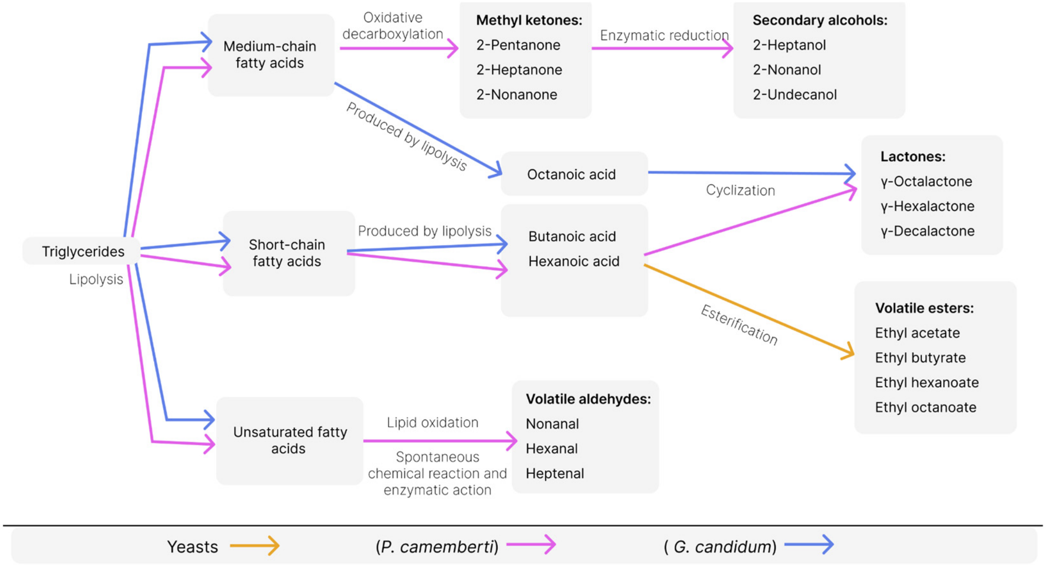

Figure 4. Fatty Acid Metabolism (Adapted from [25]).

Lipid degradation in Camembert is primarily driven by the fungus *Penicillium camemberti*, which secretes lipases and esterases responsible for hydrolyzing the triacylglycerols present in the milk fat matrix throughout cheese ripening. These processes result in the release of free fatty acids (FFA) of various chain lengths, such as butyric, lauric, myristic, palmitic, oleic, and linoleic acids, each playing distinct roles in the cheese's sensory profile [3].

Each fatty acid released during lipid metabolism contributes specifically to the sensory profile of Camembert. Butyric acid, for example, is responsible for intense cheese and rancid notes, being one of the key compounds that impart pungency to ripened cheeses. Lauric and myristic acids, which have medium-chain structures, contribute slightly sweet and buttery nuances while also influencing the cheese's texture. Palmitic and oleic acids are associated with the perception of richness and body, enhancing the characteristic creaminess of Camembert. Linoleic acid, on the other hand, can act as a precursor for secondary volatile compounds, such as aldehydes and ketones, which add complexity to the aroma with fruity, dairy, and nutty notes. The interaction between these fatty acids and the chemical reactions occurring during ripening determines the intensity and balance of the cheese's sensory attributes [7].

Lipolysis in cheese is influenced by various enzymatic sources, including enzymes naturally present in milk, microbial cultures, and enzymes added during processing. Lipoprotein lipase, found in raw milk, plays a significant role in the release of free fatty acids, directly impacting the cheese's sensory profile [23]. In cheeses made from pasteurized milk, lower enzymatic activity can limit the formation of certain aroma compounds, making the selection of starter cultures and secondary microbiota essential to compensate for this difference [27]. Additionally, lipolytic enzymes present in rennet and exogenous enzymes added during production can modulate the intensity of lipolysis, contributing to the development of specific sensory characteristics [28].

The free fatty acids (FFA) resulting from lipolysis can follow different metabolic pathways, as illustrated in Figure 5, leading to the production of volatile compounds that define the sensory characteristics of Camembert.

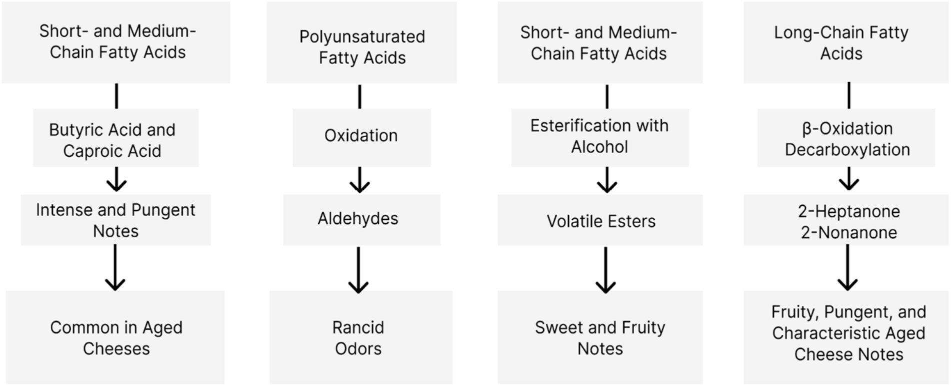

Figure 5. Pathways for the production of aroma compounds from FFA (Adapted from [3,25,29]).

Esters play a crucial role in the aroma profile of Camembert. Compounds such as ethyl acetate and methyl butyrate are responsible for fruity and sweet notes, balancing the intensity of free fatty acids. However, excessive concentrations of esters can result in overly sweet or artificial aromas, necessitating careful control of lipid metabolism and microbial activity [14].

Another important group is thioesters, such as methyl mercaptan, which contribute pungent and sulfurous notes, commonly found in washed-rind cheeses and cheeses with intense microbial activity during ripening. These compounds are formed from the metabolism of amino acids and fatty acids by specific microorganisms during maturation, including *Penicillium camemberti*, *Brevibacterium linens*, *Geotrichum candidum*, and certain species of *Lactococcus* and *Leuconostoc*, which play key roles in converting sulfur precursors into specific volatile compounds [30].

In addition to *P. camemberti*, the fungus *Geotrichum candidum* also actively participates in lipid metabolism in Camembert. This microorganism complements lipolysis by reducing bitterness, as it degrades bitter peptides generated by proteolysis. Furthermore, it enhances sulfurous notes by acting on the metabolism of amino acids and fatty acids. It also contributes to the cheese's creamy texture by modulating the lipid structure and influencing its smoothness. The combined impact of these microorganisms is essential for the sensory balance of Camembert, highlighting the importance of microbiota in shaping its characteristic aroma [6].

Technological factors, such as the type of salt used during ripening, also significantly influence lipid degradation and the formation of aroma compounds. Studies indicate that using unrefined salts can increase volatile fatty acid levels, such as octanoic acid, enhancing buttery and fruity notes. At the same time, it may reduce undesirable compounds, such as caproic acid, which is responsible for excessively pungent notes [6].

3.2.3. Odor-Active Volatiles Formed by Amino Acid Metabolism

Proteolysis represents a fundamental biochemical mechanism during the maturation of Camembert, playing a crucial role in the gradual degradation of dairy proteins, particularly caseins. This process is facilitated by an enzymatic consortium of diverse origins, including enzymes produced by *Penicillium camemberti*, *Geotrichum candidum*, and lactic acid microorganisms. The synchronized activity of these enzymes promotes the generation of peptides and free amino acids, which act as the chemical basis for flavor and aroma enhancement throughout maturation. [23].

The free amino acids formed are essential not only as basic flavor molecules (contributing to sweet, umami, and bitter notes) but also as biochemical precursors of volatile compounds responsible for Camembert's characteristic aroma [31]. The subsequent metabolism of these components involves reactions such as transamination, decarboxylation, deamination, and oxidation, leading to the formation of alcohols, carboxylic acids, esters, and volatile sulfur compounds. These pathways are highly influenced by environmental conditions such as temperature, humidity, and pH, as well as the composition of the surface microbiota. The main transformations and their sensory contributions can be visualized in Figure 6, which illustrates the metabolic routes involved in the conversion of amino acids into aroma compounds.

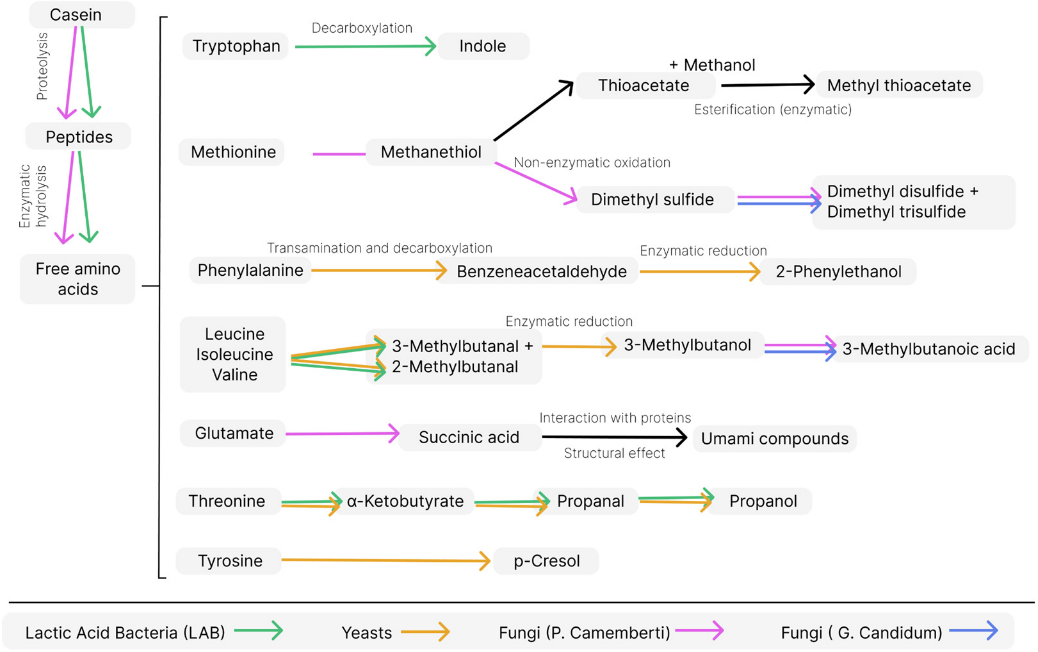

Figure 6. Pathways for the production of aroma and flavor compounds from amino acids.

Among the precursor amino acids, methionine and cysteine play a prominent role, as they give rise to volatile sulfur compounds, which are highly specific to white mold cheeses. Methionine metabolism leads to the formation of methanethiol, which is subsequently oxidized to dimethyl disulfide and dimethyl trisulfide—compounds with extremely low perception thresholds, responsible for the pungent, sulfurous, and ammoniacal notes of Camembert's rind [32]. In contrast, other amino acids, such as glutamate, do not contribute to aroma directly but are involved in the formation of non-volatile flavor compounds, such as succinic acid and umami-related metabolites. These molecules play a key role in taste perception rather than olfactory characteristics, and therefore contribute to the overall flavor but not to the aroma of the cheese [23,31].

Additionally, aroma and branched-chain amino acids contribute to the formation of alcohols and aldehydes responsible for floral, fruity, and malty notes, adding layers of complexity to the cheese's aroma. Table 3 summarizes the main metabolic pathways of amino acids, highlighting the compounds formed and their sensory relevance.

Table 3. Metabolic pathways of amino acids, formed compounds, and their sensory relevance (Adapted from [16,27,30,33,34]).

Amino Acid Precursor	Conversion Step	Formed Compounds	Sensory Characteristics	Sensory Importance in Camembert
Methionine	Deamination and enzymatic conversion via transaminases	Methanethiol, Dimethyl disulfide,	Sulfurous, pungent, and ammoniacal notes	Typical rind aroma, onion and sulfur notes

		Dimethyl trisulfide		
Cysteine	Similar reactions via sulfur metabolism	Volatile sulfur compounds	Similar to methionine	Complements the sulfurous profile of Camembert
Phenylalanine	Transamination and decarboxylation	Phenylethanol, Benzaldehyde	Floral and sweet notes	Contributes to floral/fruity notes
Lysine	Decarboxylation by bacterial decarboxylase	Cadaverine	Metallic and pungent aroma at high concentrations	Related to sensory defects in excessive ripening
Arginine	Decarboxylation via the arginine deiminase system	Ornithine → Cadaverine	Similar to cadaverine	Can indicate uncontrolled fermentation
Glutamine and Asparagine	Enzymatic deamination	Ammonia (NH_3)	Ammoniacal aroma; regulates pH	Essential for creamy texture and microbiological balance

This amino acid metabolism is strongly influenced by ripening conditions, including the temperature and humidity of the ripening chamber, which affect proteolytic activity and the rate of protein breakdown. Additionally, the pH of the cheese surface regulates the activity of key enzymes such as aminopeptidases and decarboxylases. Finally, the composition of the brine and the rind influences moisture retention and enzyme diffusion throughout the cheese matrix, directly impacting aroma and texture development.

Studies indicate that fine-tuning these parameters allows for the customization of the aroma profile, promoting the formation of desirable compounds while minimizing metabolites associated with sensory defects [34,35]. This ability to modulate the ripening process is particularly relevant for the industry, enabling adaptation to regional preferences and the creation of products with specific aroma profiles [13].

3.3. Role of Microbiota in the Ripening of Camembert Cheese

The ripening process of Camembert cheese is a complex phenomenon mediated by the interaction between filamentous fungi, LAB and yeasts. These microorganisms carry out crucial biochemical transformations that shape the desired sensory characteristics, such as aroma, texture, and flavor. The coordinated action of the microbiota facilitates the breakdown of proteins, lipids, and carbohydrates, leading to the formation of essential volatile and non-volatile compounds that define the final sensory profile [3].

3.3.1. Role of Penicillium Camemberti

During ripening, *P. camemberti* secretes proteolytic and lipolytic enzymes that play essential roles in the breakdown of macromolecules, releasing peptides and free amino acids. These amino acids are metabolized into secondary volatile compounds, which contribute to specific aroma notes that define Camembert's sensory profile [30].

One of the most notable processes is the metabolism of sulfur-containing amino acids, such as methionine, which leads to the formation of volatile sulfur compounds—methanethiol, dimethyl disulfide, and dimethyl trisulfide—responsible for the pungent, ammoniacal, and sulfurous notes characteristic of Camembert [14].

Additionally, the deamination of various free amino acids, such as glutamine and asparagine, results in the release of ammonia, which contributes to an increase in the pH of the cheese surface. This pH increase is essential for developing the creamy texture typical of Camembert's interior, while also influencing enzymatic activity and the microbial composition of the rind.

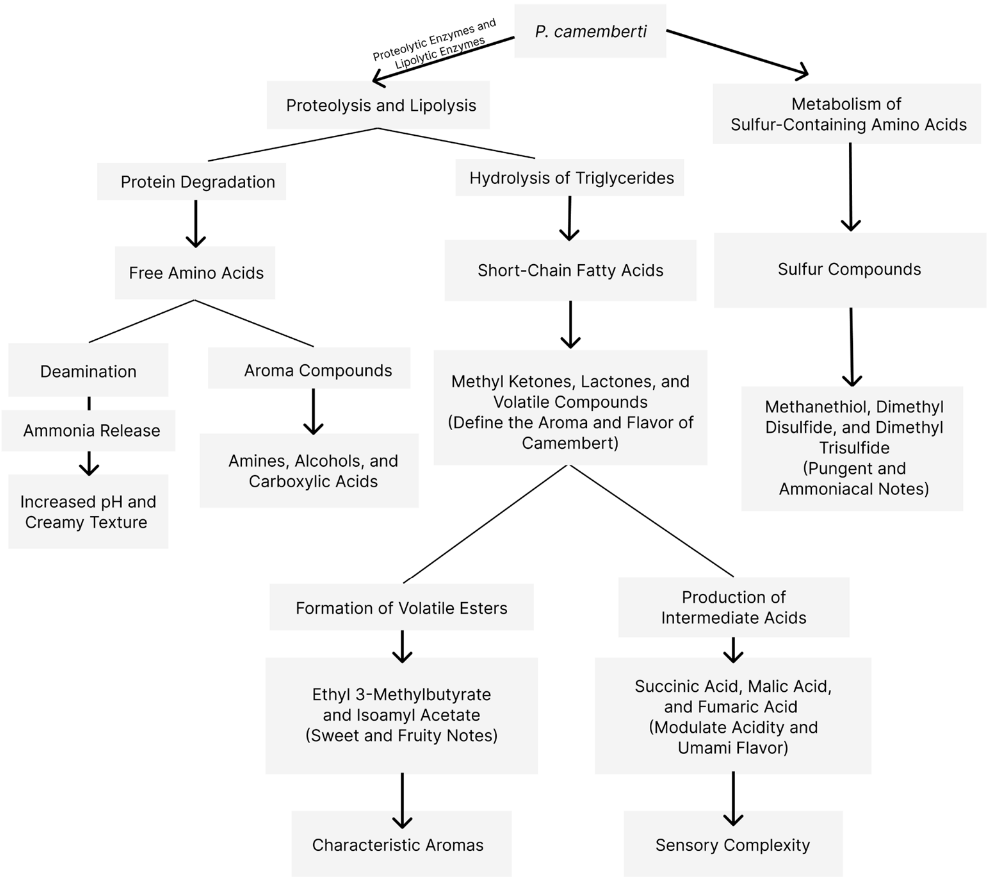

Figure 7. Metabolic pathways for the production of volatile (aroma) and non-volatile (flavor and texture) compounds by *Penicillium camemberti* (Adapted from [14,30,33,35–38]).

3.3.2. Role of Lactic Acid Bacteria (LAB)

Lactic acid bacteria (LAB), such as *Lactococcus lactis*, *Lactococcus cremoris*, and *Leuconostoc mesenteroides*, play a fundamental role in the early stages of Camembert ripening. These bacteria ferment lactose present in milk, converting it into lactic acid, which promotes the acidification of the cheese matrix. This acidification creates a hostile environment for undesirable microorganisms, favoring the growth of specific cultures, including ripening fungi such as *Penicillium camemberti* [28,39].

Additionally, LAB play a crucial role in generating aroma precursor compounds, such as diacetyl and acetoin, which originate from citrate metabolism. These compounds are subsequently metabolized by *Penicillium camemberti*, contributing to the characteristic aroma balance of Camembert [39]. LAB also participate in the breakdown of residual lipids, helping to reduce rancid notes by converting aldehydes and FFA into volatile esters and secondary alcohols, such as ethyl acetate and 2-butanol [11,28].

Another important function of LAB involves the metabolism of FFA, particularly through transamination and decarboxylation, leading to the formation of higher alcohols, aldehydes, and sulfur compounds that directly impact the aroma profile [40]. The main metabolic pathways involving LAB and their interaction with *Penicillium camemberti* can be observed in the Flowchart in Figure 8, which illustrates the synergistic contribution of these microorganisms to the sensory complexity of Camembert.

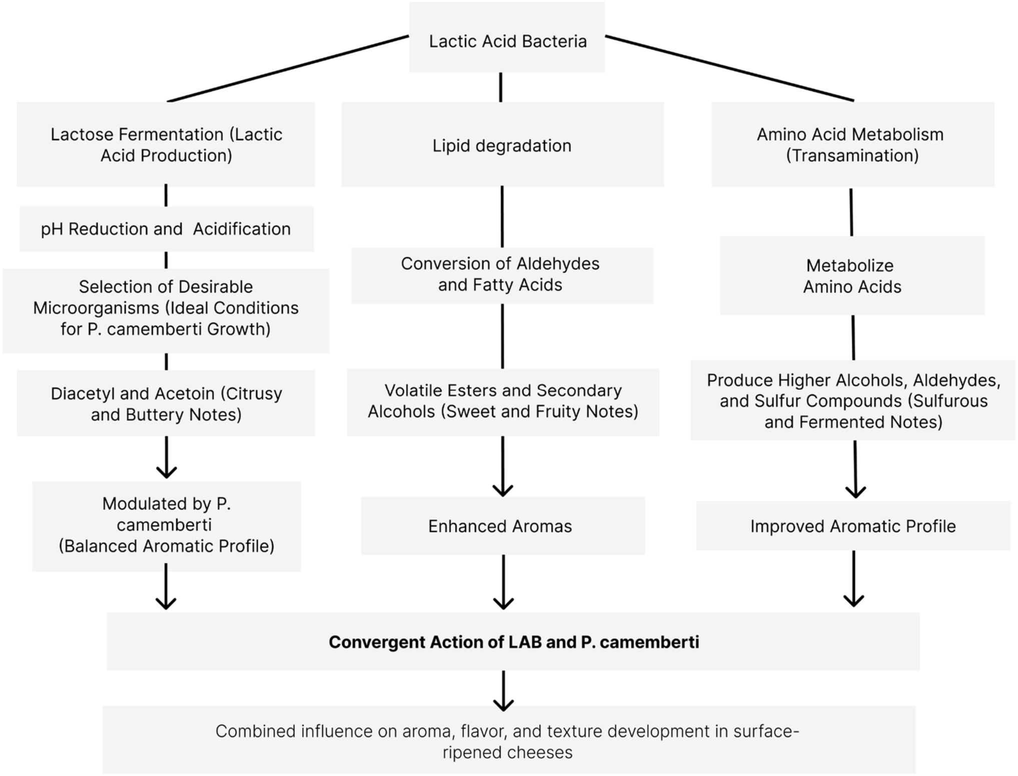

Figure 8. Synergistic pathways of aroma, flavor, and texture development in surface-ripened cheeses involving Lactic Acid Bacteria and *P. camemberti* (Adapted from [26,27,33,41]).

The symbiotic relationship between LAB and *P. camemberti* is crucial for the development of Camembert cheese. LAB produce lactic acid, creating an initially acidic environment. *P. camemberti* then consumes this acid, releasing ammonia and increasing the pH, which favors the growth of other microbial cultures and promotes uniform ripening [16].

3.3.3. Role of Yeasts

Although often less emphasized, yeasts play essential roles in the sensory development of Camembert, primarily through the metabolism of residual sugars, lactate, and lipids, resulting in compounds that enhance the aroma and balance the acidity of this cheese [42]. Among the predominant species, *Debaryomyces hansenii* contributes to cheese deacidification and facilitates the growth of filamentous fungi such as *Penicillium camemberti* [27]. Meanwhile, *Yarrowia lipolytica* participates in lipid hydrolysis, producing volatile compounds such as esters and aldehydes, which add fruity and floral notes to the cheese [14].

The synergy between LAB, *Penicillium camemberti*, and yeasts is fundamental to Camembert's sensory profile. This interaction promotes the formation of aroma compounds derived from carbohydrates, such as ethyl lactate, which adds sweetness and complexity to the aroma.

Additionally, *Geotrichum candidum* contributes to bitterness reduction and the formation of sulfur compounds, influencing both the aroma and texture of the cheese [43].

3.4. Methods for the Analysis of Volatile Compounds

The identification of volatile compounds in Camembert presents a challenge due to their structural complexity and the concentration variations of each component. The sensitivity of the human olfactory system surpasses that of many instrumental systems, requiring the application of pre-concentration and volatile extraction techniques before analysis [4]. The high water content in cheese can dilute these aroma compounds, making their detection by CG-MS more difficult [44], while the presence of proteins, lipids, and carbohydrates can directly interfere with compound specificity and analysis [3].

In recent years, advancements in chromatographic and microextraction techniques, such as SPME, have enabled a more detailed characterization of the volatile profile of ripened cheeses [45]. However, analyzing these compounds remains challenging due to the synergistic and antagonistic interactions occurring within the cheese matrix, which complicate the isolated evaluation of each volatile compound’s impact on the final perceived aroma [16].

On the other hand, identifying volatile compounds alone is not sufficient to fully understand the aroma of Camembert. Many instrumentally detected compounds have no direct sensory relevance, while others, present at extremely low concentrations, exert a strong olfactory impact [7]. To bridge this gap, techniques that combine instrumental analysis with sensory evaluation are indispensable, such as GC-O, which directly correlates each detected compound with its actual olfactory perception [9].

The sensory characterization of Camembert can also be enhanced using descriptive methodologies, such as Quantitative Descriptive Analysis (QDA), which describes sensory attributes in standardized terms, and consumer preference mapping, which associates different aroma profiles with target consumer accessibility [5,13].

Thus, a comprehensive understanding of Camembert’s aroma profile requires an integrated approach that combines analytical techniques for identifying chemically and odor-active volatile compounds with sensory methods to validate human perception. Table 4 presents an overview of these approaches, highlighting their specific applications in Camembert analysis, along with their key advantages and limitations.

Table 4. Analytical and sensory techniques for characterizing volatile and odor-active compounds in Camembert cheese (Adapted from [3–5,46–48]).

Technique	Description	Applications in Camembert	Advantages	Limitations
Gas Chromatography (GC)	Separation technique for identifying volatile compounds based on their interaction with the stationary and mobile phases.	Initial identification of alcohols, esters, short-chain fatty acids, and sulfur compounds.	High resolution and efficiency in compound separation.	Unable to directly identify odor-active compounds.

Gas Chromatography-Mass Spectrometry (GC-MS)	Combines GC with mass spectrometry for structural analysis and quantification of volatile compounds.	Detailed characterization of the volatile profile and initial correlation with sensory descriptors.	High sensitivity and precise identification.	Requires sophisticated equipment and longer analysis time.
Gas Chromatography-Olfactometry (GC-O)	Technique combining CG-O with sensory evaluation by a trained assessor at the olfactory detector.	Identification of odor-active compounds and their direct sensory contribution.	Allows direct correlation between volatile compounds and their olfactory perception.	Requires a trained panel and may be influenced by subjective perception.
Solid-Phase Microextraction (SPME)	Pre-concentration technique using sorbent fibers to capture volatiles before GC or GC-MS analysis.	Enhances the detection of compounds present at low concentrations in the cheese matrix.	Fast, simple, and non-destructive method.	Requires optimization for each matrix and analytical condition.
Quantitative Descriptive Analysis (QDA)	Formal sensory evaluation by a trained panel to describe and quantify aroma, flavor, and texture attributes.	Standardized description of Camembert's sensory profile, including its key aroma notes.	Enables mapping of key attributes and sample comparison.	Inherent subjectivity of human sensory analysis.
Consumer Preference Mapping	Consumer testing to assess preferences for different aroma profiles.	Identifies which volatile profiles are most accepted or desired by different consumer groups.	Links chemical and sensory profiles to product accessibility.	Lower technical precision and dependent on the selected consumer sample.

Recent technological advances have driven the development of innovative approaches for analyzing volatile compounds and evaluating aroma in cheeses like Camembert. These new methodologies combine advanced chemical detection techniques, high-precision sensing, and data modeling tools, enabling a more comprehensive and integrated understanding of the cheese's sensory profile [4,16].

Monitoring the volatile compounds of Camembert is essential to ensuring its sensory and commercial quality. Changes in the aroma profile may indicate microbiota imbalances, deviations in the ripening process, or variations in raw materials. Emerging technologies, such as electronic sensors (electronic noses), allow for rapid and non-destructive analysis of volatile compounds during production, enabling early detection of ripening deviations and contributing to quality standardization [14]. This continuous monitoring is also crucial for identifying sensory defects or microbial contaminants, ensuring not only sensory stability but also product safety and consumer satisfaction [3].

Additionally, metabolomics and metagenomics platforms provide a holistic view of the microbiota and its influence on the formation of volatile compounds during ripening [14]. Emerging techniques, such as ion mobility spectrometry (IMS), enable rapid, direct analysis of food matrices, while electronic noses simulate human olfactory perception, offering a direct technological interface for real-time quality control [49,50].

Table 5 summarizes the main innovative approaches used for characterizing aroma compounds in Camembert, highlighting their principles, applications, and benefits.

Table 5. Innovative Approaches for the Analysis of Aroma Compounds (Adapted from [4,14,16,49,50]).

Innovative Technique	Description	Applications in Camembert
Nuclear Magnetic Resonance Spectroscopy (NMR)	Identifies and quantifies volatile and non-volatile metabolites, providing insights into metabolic processes.	Highlights the formation of aroma precursor compounds, such as amino acids and fatty acids.
Metabolomics and Metagenomics Platforms	Correlate the cheese microbiota with volatile compounds produced during ripening.	Identify critical metabolic pathways and potential technological adjustments to optimize the sensory profile.
Electronic Sensors (Electronic Nose)	Devices that simulate human olfactory perception, detecting and classifying volatile compounds in real time.	Monitor cheese quality during production and ripening, providing rapid and consistent data.

Although the analysis of volatile compounds in white mold cheeses such as Camembert already involves a wide range of chromatographic, spectrometric, and sensory techniques, certain relevant methodologies remain underexplored for this specific product. One such technique is AEDA, which combines GC-O with successive dilutions of aroma extracts, allowing for the objective ranking of odor-active compounds based on the persistence of their odors throughout the dilutions. This approach, widely used in studies of fermented products and complex foods such as dairy products, has proven highly effective in characterizing key compounds in cheeses of different origins, although its specific application to Camembert remains scarce [51].

Another valuable tool is the determination of the OAV, a parameter that relates the concentration of each volatile compound to its olfactory perception threshold, providing a quantitative assessment of the relative importance of each substance to the overall aroma. This technique has already been used in aroma studies of various dairy and fermented products, including soft cheeses, though its systematic application to Camembert is not yet well documented [52].

Additionally, complementary olfactometric evaluation techniques, such as Osme, which records the perceived odor intensity of each compound during chromatographic elution, and the GC-Sniffing Port, used as a descriptive sensory screening tool, are well-established methodologies for analyzing complex food matrices. These methods have already been applied in studies involving aged and fermented cheeses [53].

Another innovative technique with potential for future exploration is IMS, an analytical tool capable of performing rapid and sensitive real-time analyses of volatile compositions. Despite its increasing application in fermented foods, there are no well-documented records of its specific use in white mold cheeses, presenting a methodological opportunity for improving volatile monitoring throughout ripening and for developing real-time quality control tools [54].

However, its dedicated application in studies exclusively focused on Camembert and Brie remains limited. This lack of specific research highlights a methodological gap, suggesting that adopting these tools in future studies could significantly enhance our understanding of the relationship between chemical composition and sensory perception in traditional white mold cheeses such as Camembert.

3.5. Effect of Processing Conditions on the Formation of Volatile Compounds and the Aroma Profile of Camembert

Camembert cheese is highly valued for its unique aroma profile, which results from complex interactions between microbiota, biochemical processes, and ripening conditions. In the industry, optimizing these factors is essential to ensure consistency in quality, meet consumer preferences, and explore new market opportunities [42].

Technological and processing factors, such as the type of salt used during ripening, directly affect the formation of volatile compounds. The use of non-organic salts, such as Himalayan pink salt, has been shown to enhance the levels of carboxylic acids and alcohols, improving sensory notes in aged cheeses [6]. Emerging technologies, such as X-ray irradiation, are also being investigated as a strategy to improve the volatile profile of aged cheeses, offering new perspectives for aroma preservation and enhancement [4].

The ripening of Camembert is a highly sensitive process, influenced by microbiota, environmental conditions, and milk formulation. Precise adjustments in parameters such as temperature, humidity, and oxygenation throughout ripening directly impact aroma development, promoting the proteolytic and lipolytic activity of microorganisms like *Penicillium camemberti*, resulting in a more complex aroma profile [33].

The use of selected cultures of *Penicillium camemberti* and genetically adapted LAB allows for the targeted production of desirable volatile compounds, such as methyl ketones and esters, while reducing undesirable compounds, leading to a more balanced and pleasant sensory profile [27]. Studies have shown that volatile profile modulation can be fine-tuned through microbial culture selection and ripening condition control. For example, species of Monascus and auxiliary cultures can increase levels of aroma compounds such as butanediol and 2-undecanone, contributing to distinct sensory profiles with floral and fruity notes [3].

Additionally, the introduction of digital and automated tools, such as automated fermenters and digitally controlled ripening chambers, enables precise process control. These systems can be integrated with electronic sensors and artificial intelligence algorithms, allowing for real-time monitoring and prediction of aroma profile development [16].

3.5.1. Innovations in the Ripening Process

Innovations in the ripening process of Camembert aim not only to optimize sensory quality and industrial reproducibility but also to create strategic opportunities for product innovation and diversification in the global market. The customization of the aroma profile can be used as a tool to develop Camembert varieties with specific sensory appeals, such as cheeses with intensified fruity, floral, or ammoniacal notes, tailored to regional consumer preferences [5].

In this context, the growing appreciation for artisanal and gourmet products strengthens Camembert’s positioning as a premium product, especially when associated with limited editions or certification under a Protected Designation of Origin (PDO), reinforcing the link between terroir and specific sensory characteristics [14].

Innovations also include the incorporation of functional or probiotic ingredients during production, addressing the increasing demand for foods that combine flavor with health benefits. These products, in addition to promoting well-being, can exhibit distinctive aroma profiles, expanding market segmentation possibilities [27].

At the same time, the use of electronic sensors and automated systems has gained traction as a tool for real-time monitoring of the ripening process, enabling proactive correction of deviations and directly contributing to final product consistency [14]. The combination of aroma profile customization and digital tools also facilitates the development of premium and differentiated products, driving innovation in the dairy sector [5].

4. Conclusions and Future Perspectives

A critical analysis of the techniques used to characterize volatile compounds and their relationship with sensory perception in Camembert cheese reveals significant technical challenges for both industry and scientific research. The complexity of the cheese matrix, combined with the diversity of volatile compounds and the variability of their concentrations, presents ongoing difficulties in achieving a precise and reproducible analysis of the aroma profile.

From an analytical perspective, combining traditional chromatographic techniques with sensory approaches and innovative tools such as electronic sensors and metabolomic platforms represents a promising strategy to overcome these limitations. However, the effective integration of these techniques into industrial routines still requires robust validation and the harmonization of analytical and sensory protocols.

Another key challenge is the controlled customization of the aroma profile, which would allow for the development of products tailored to the preferences of different consumer markets. To achieve this, it is essential to deepen our understanding of the interactions between microbiota, cheese matrix biochemistry, and processing conditions, as well as to foster stronger synergy between academic research and industrial innovation. In this context, expanding knowledge on microbiota interactions, biochemical processes, and technological conditions positions Camembert as a relevant model for developing new technologies applicable to other fermented foods. This integrated approach, which connects fundamental science, process technology, and market strategies, highlights the central role of scientific research in responding to the growing demand for high-quality sensory products with complex aroma profiles and guaranteed traceability.

Despite advances in understanding the ripening process, several scientific gaps remain, offering opportunities for future studies focused on a deeper characterization of Camembert’s aroma. Among these gaps, the following stand out:

Unexplored Metabolic Pathways: Recent studies using gas chromatography-olfactometry (GC-O) have detected sensorily relevant peaks that have yet to be fully identified or whose biochemical origins remain unknown [43]. Volatile sulfur compounds, responsible for pungent and ammoniacal notes, are a classic example of metabolites whose formation may involve alternative pathways that remain underexplored, particularly under specific ripening conditions such as low oxygenation or osmotic stress [42]. Similarly, lactones and nitrogenous heterocyclic compounds, associated with fruity and toasted notes, are also detected, but their complete metabolic pathways are still under investigation [16].

Specific Microbial Interactions: The application of metagenomic and metabolomic tools has provided a new level of understanding regarding the interactions between microorganisms in Camembert and their direct influence on aroma compound formation [55]. For example, studies show that the initial lipolytic activity of *Geotrichum candidum* modifies the availability of substrates for *Penicillium camemberti*, altering the production of methyl ketones and directly impacting the aroma profile [42]. Additionally, lesser-studied species, such as *Debaryomyces hansenii*, play a significant role in detoxifying the ripening environment and producing alcohols and esters, contributing to characteristic fruity and fermented notes [16]. These microbial interactions remain underexplored under industrial conditions, representing a promising field for targeted optimization of the sensory profile.

Effects of Technological Adjustments: Factors such as temperature, humidity, and milk composition directly impact the formation of volatile compounds and, consequently, the sensory profile of Camembert [16]. Lower temperatures hinder lipolytic and proteolytic activity, resulting in a milder and less pungent aroma, while moderate temperatures accelerate the formation of methyl ketones and sulfur compounds, which are characteristic of Camembert's typical aroma [56]. The relative humidity of the ripening chamber regulates rind formation and the balance between yeasts and fungi, favoring milder profiles under high humidity or more intense, aged characteristics under low humidity conditions [16]. Meanwhile, milk composition, including fat and protein content, determines the availability of essential metabolic precursors, directly influencing the formation of key aroma compounds such as esters, lactones, and sulfur derivatives [56].

Innovative Approaches for Chemical-Sensory Correlation: Although Camembert has been extensively analyzed through chromatographic and spectrometric methods, the use of approaches that directly correlate chemical composition with sensory perception remains limited for this specific type of cheese. Techniques such as AEDA, which combines serial dilutions of aroma extracts with sensory evaluation via GC-O, and OAV determination, which prioritizes key compounds based on their relative concentration and perception thresholds, are widely applied in other fermented products but remain underexplored in white mold cheeses, including Camembert [51].

Additionally, methods such as Osme, which records the perceived intensity of each compound during chromatographic elution, and the systematic application of GC-Sniffing Port as a sensory screening tool, could provide groundbreaking insights into compounds responsible for Camembert's distinctive sensory characteristics [53]. When combined with targeted metabolomics and artificial intelligence tools applied to sensory analysis, these techniques open new possibilities for precise quality control and aroma profile customization, with potential impacts on both gourmet product innovation and industrial standardization.

Given these research gaps and opportunities, further exploration of new metabolic pathways, synergistic microbial interactions, targeted technological adjustments, and advanced chemical-sensory techniques represents not only a scientific opportunity but also an applied strategy to enhance sensory quality control and drive innovation in the production of Camembert and other surface-ripened cheeses.

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Abbreviations

The following abbreviations are used in this manuscript:

GC-MS	Gas Chromatography-Mass Spectrometry
GC-O	Gas Chromatography-Olfactometry
SPME	Solid-Phase Microextraction
GC	Gas Chromatography
AEDA	Aroma Extract Dilution Analysis
OAV	Odor Activity Value
LAB	Lactic Acid Bacteria
FFA	Free Fatty Acids
QDA	Quantitative Descriptive Analysis
IMS	Ion Mobility Spectrometry
NMR	Nuclear Magnetic Resonance Spectroscopy

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