

Review

Integrated Insights into Structural and Flavor Functions of Milk Fat in Cheese Systems: Implications for Fat Reduction and Replacement Strategies

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Abstract

The increasing demand for sustainable and health-oriented dairy and alternative products has enhanced interest in reducing or modifying fat in cheese systems. However, such modifications often lead to undesirable changes in texture and flavor, highlighting the multifunctional roles of milk fat within the cheese matrix. Rather than serving solely as a compositional component, milk fat contributes fundamentally to structure organization and flavor development through its physicochemical properties, interactions with the protein network, and lipid-derived pathways. This review examines these roles from a mechanistic perspective and evaluates emerging lipid structuring approaches for texture modulation, while also discussing complementary approaches with potential to address flavor attributes. Collectively, it provides insights for rational formulation and guides future research toward the design of improved dairy and alternative cheese products.

Keywords: milk fat; cheese structure; cheese flavor; fat reduction; fat replacement; lipid structuring

1. Introduction

Cheese is a complex dairy product formed through the coagulation of milk proteins, primarily casein, via enzymatic or acidification processes [1]. Interactions among proteins, lipids, and other components within the cheese matrix regulate key functional and sensory attributes, which are critical determinants of consumer acceptance [2]. Among these components, milk fat critically influences both structural organization and flavor development [3–5]. The physicochemical properties of milk fat, including its heterogeneous triacylglycerol composition, polymorphic crystallization behavior, and melting characteristics, determine the mechanical properties and stability of the cheese matrix [6–8]. Within the protein matrix, fat droplets act as active fillers that modulate viscoelasticity and network organization through their interactions with the surrounding caseins [9]. In addition, milk fat regulates the retention and release of hydrophobic flavor compounds while also contributing to aroma generation through lipolysis and subsequent volatile formation [10]. Collectively, these structural and biochemical functions make milk fat a key determinant of texture and flavor formation in cheese systems.

Due to these multifunctional roles, reduction or replacement of milk fat frequently alters cheese functionality. This challenge is particularly evident in reduced-fat cheeses, cheese analogs, and plant-based cheese alternatives, where partial or complete replacement



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of milk fat often leads to poor meltability, texture and flavor properties [11–13]. These limitations are associated with alterations in fat physicochemical behavior and lipid-derived flavor development following fat modification or replacement [11–13].

Consequently, increasing demand for plant-based and analog cheese products, together with growing interest in reduced-fat dairy products, has intensified efforts to modify, reduce, or replace milk fat in cheese systems [11,12,14,15]. Fat-structuring strategies, including oleogelation, interfacial structuring, emulsion-based systems and interesterification, are mainly applied to improve textural properties [16]. However, modification of the fat phase may still negatively affect flavor development and aroma retention [16]. Therefore, complementary approaches such as microbial fermentation and encapsulation have also been investigated to compensate for sensory limitations and improve cheese-like flavor properties.

These limitations highlight a fundamental issue: the functionality of milk fat is influenced not only by its composition but also by its dynamic behavior within the cheese matrix and ongoing biochemical transformations [17,18]. However, existing research has predominantly focused on developing alternative or reduced-fat cheese systems through formulation strategies designed to approximate desired structural and sensory properties [11,13,15,19]. In contrast, the multifunctional roles of milk fat itself, particularly lipid physicochemistry, lipid–protein interactions, and lipid-mediated flavor development, are often investigated separately rather than as interconnected contributors to cheese functionality. Consequently, the integrated perspective on the role of milk fat in regulating cheese structure, textural properties, and flavor development remains insufficiently developed.

In this context, this review provides an integrated overview of milk fat functionality in cheese systems, with emphasis on its contributions to cheese structure, textural properties, and flavor development (Figure 1). The review summarizes current understanding of milk fat physicochemistry, lipid–protein interactions, and lipid-derived aroma formation, while also discussing emerging technologies designed to modify or structure the fat phase and their current limitations. Collectively, this review aims to provide a mechanistic perspective on milk fat behavior in dairy cheese systems and its implications for cheese reformulation strategies involving fat reduction or replacement.

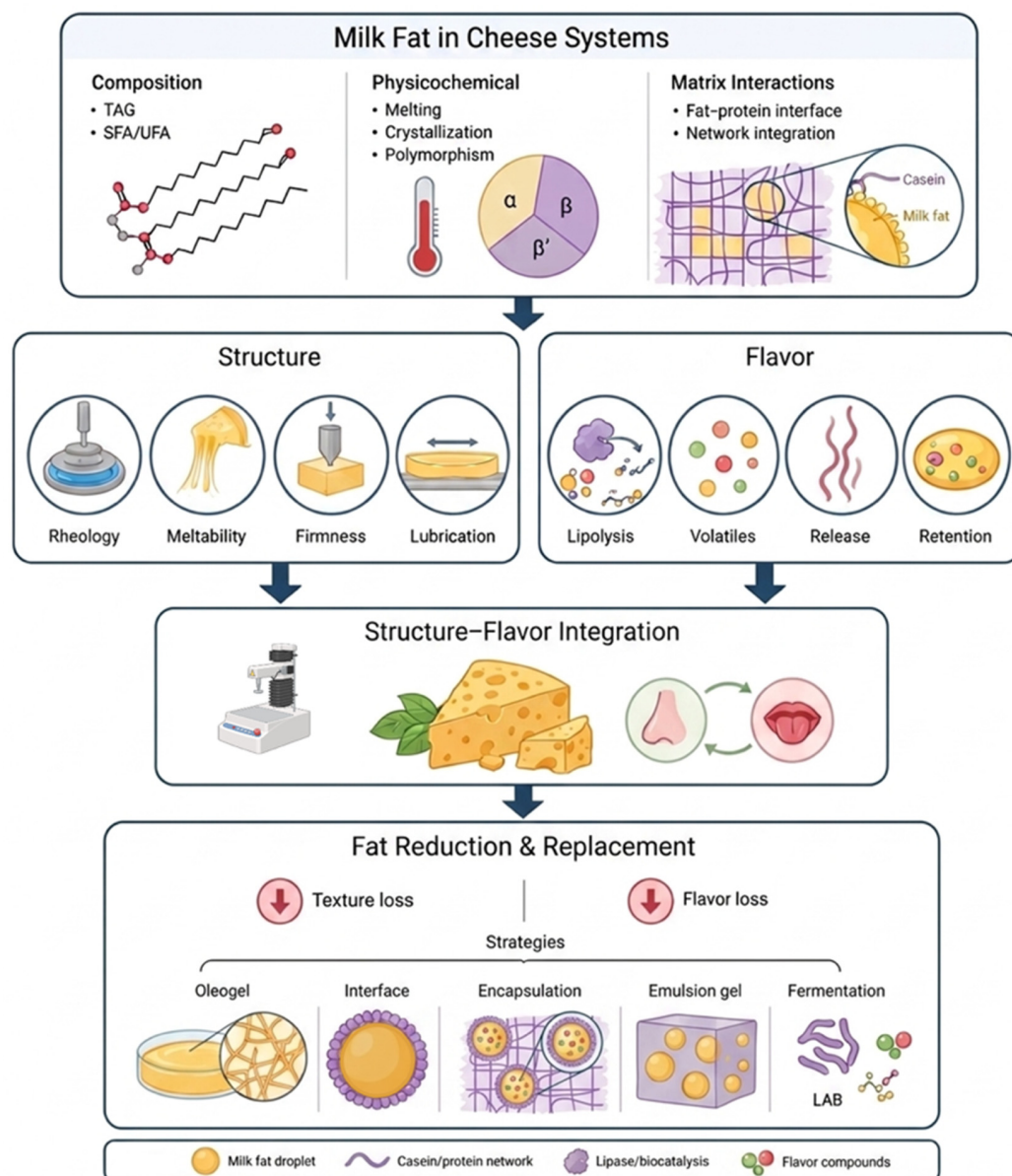


Figure 1. Milk fat roles in structure–flavor development and implications for fat reduction in cheese.

2. Literature Search and Selection

A literature search was carried out using Google Scholar and Web of Science. Core keywords related to milk fat functionality, cheese structure, texture, and flavor development were used individually and in combination, including “milk fat”, “milk fat globule”, “fat polymorphism”, “fat crystallization”, “lipolysis”, “microstructure”, “rheology”, “meltability”, “functionality”, “cheese flavor”, “cheese matrix”, “homogenization”, “protein-fat interactions”, and “cheese sensory”. Additional keywords related to alternative cheese systems and technological applications were also included for comparative analysis of fat-structuring approaches, including “fat replacement”, “reduced-fat cheese”, “plant-based cheese”, “cheese analogue”, “oleogelation”, “interesterification”, “pickering emulsion”, “emulsion-filled gel”, and “fat structuring”.

The literature search was primarily conducted between March 2025 and March 2026, with additional recently published studies included where relevant. The review primarily focused on peer-reviewed articles published between 2000 and 2026, although earlier seminal studies were included where relevant. The inclusion criteria comprised studies investigating the physicochemical, structural, rheological, sensory, and flavor-related roles

of milk fat in cheese systems, as well as fat modification and replacement strategies in dairy and alternative cheese products. Exclusion criteria included duplicate records, studies lacking sufficient experimental detail, and studies not directly related to cheese fat functionality, texture formation, flavor development, or fat reduction and replacement strategies.

3. Structural Role of Dairy Fat in Cheese

3.1. Physicochemical Properties of Milk Fat

Milk fat is composed mainly of triacylglycerols (TAGs) (98%), with other constituents including phospholipids (1–2%), sterols, diacylglycerols, fat-soluble vitamins, carotenoids, and free fatty acids (<1%). Milk fat can crystallize into three principal polymorphic forms (α , β' , and β), which differ in stability, crystal packing, and functional properties [20–22]. These polymorphs determine the crystal organization and functional behavior of milk fat in its solid state [22]. The α form is the least stable polymorph with the lowest melting point and is typically formed during the rapid cooling [23–25]. In contrast, the β' polymorph is characterized by fine, needle-like structures that form dense networks and entrap more liquid oil [23–25]. This structure contributes to improving plasticity, spreadability, and smooth texture in fat-based systems such as margarine [24–26]. The β form is the most stable polymorph, characterized by the highest melting point and crystal packing density [23,25,27]. These polymorphs undergo an irreversible transformation from α to β' and ultimately β , resulting in progressively more stable crystal states [6,28].

Milk fat also shows complex thermal behavior due to the heterogeneous melting of its TAG fractions [29,30]. As temperature increases, progressive melting of TAG fractions reduces the solid fat content (SFC), thereby affecting firmness, spreadability, and mouth-feel [29]. Variations in crystal morphology (flaky, columnar, or acicular) further influence the physical stability and mechanical behavior of the fat phase, thereby determining the textural properties such as plasticity and hardness [6]. Milk fat naturally favors the formation of the β' polymorph, as the unstable α form rapidly transforms and the β form is rarely observed due to its association with large crystal formation and undesirable sand-like texture [27]. The predominance of the β' polymorphic form in anhydrous milk fat (AMF) facilitates the formation of smooth, cohesive structures in cheese [27]. This crystalline behavior contributes to key textural properties such as plasticity and spreadability, making milk fat suitable for cheese applications. Higher proportions of low-melting α crystals are associated with increased free oil release and reduced apparent viscosity in cheese matrix [8]. Gliguem et al. also indicated that milk fat polymorphism improves matrix cohesion and mechanical strength in processed cheese systems [31]. Moreover, fat crystallization enhances the interfacial anchorage between fat droplets and the surrounding protein network, thereby increasing cheese firmness at low temperatures [31]. Milk fat polymorphism in cheese systems is strongly influenced by crystallization kinetics during processing, thereby affecting textural attributes such as firmness and viscoelasticity [31–33]. Processing parameters, particularly cooling rate, crystallization temperature, agitation and homogenization intensity, directly regulate nucleation behavior, crystal growth, and polymorphic organization [32,34–38]. Rapid cooling promotes fast nucleation and incorporation of different TAGs into crystal structures [32,39], thereby favoring formation of unstable α polymorphs, whereas slow cooling facilitates progressive TAG rearrangement and development of more stable β' structures [32,36,39]. Accordingly, anhydrous milk fat (AMF) cooled at 10 °C/min formed crystals smaller than 250 μm^2 , whereas slow cooling at 0.1 °C/min produced crystals ranging from 50 to 950 μm^2 [32]. In processed cheese, fat droplets (~0.7 μm) remain partially crystallized below 14.5 °C, consisting of coexisting liquid and solid TAG fractions [31]. Gliguem et al. further reported that slow (0.5 °C min^{−1}) and intermediate (1–2 °C min^{−1}) cooling rates promoted progressive increase in G' and G''

values during cooling, resulting in greater structural reinforcement and firmer processed cheese matrices [31]. Such effects are highly relevant in industrial cheese manufacture, where cooling protocols (e.g., water-bath cooling of processed Mozzarella blocks) are used to regulate fat solidification, polymorphic evolution, and rheological properties [40]. Agitation and shear forces generated during curd stirring, pumping, mixing, homogenization and pasta filata stretching further influence milk fat crystallization behavior. Agitation enhances primary nucleation, whereas higher shear forces accelerate secondary nucleation through crystal fragmentation, resulting in increased crystal number and reduced crystal size [41]. Shear may further accelerate polymorphic transition by promoting formation and segregation of smaller crystallites that act as additional nucleation sites, while simultaneously altering crystal and liquid-phase composition during crystallization [42]. Kaufmann et al. demonstrated that high shear rates ($74\text{--}444\text{ s}^{-1}$) accelerated the α -to- β' transition in AMF compared with static conditions [43]. However, the influence of shear remains strongly dependent on crystallization conditions. Grall and Hartel reported that high shear promoted smaller crystal formation at 20 and 30 °C, whereas the opposite behavior was observed at 15 °C, suggesting that crystal habit and structural sensitivity to shear vary with thermal history [44].

Homogenization may further alter milk fat polymorphism by modifying droplet size, interfacial organization, and crystallization environment. Ramel and Marangoni reported that embedding AMF droplets within cheese matrices promoted formation of the more stable β polymorph compared with bulk fat systems dominated by β' crystals [34]. These findings suggest that physical confinement within the surrounding protein matrix, rather than homogenization alone, regulates β polymorph formation by restricting TAG mobility and promoting thermodynamically stable crystal structures. The crystallization behavior of milk fat is also influenced by its physical state during solidification, specifically, whether AMF crystallizes in bulk or as dispersed droplets within a protein matrix. Under confinement, melting transitions become well separated, showing distinct low-/middle- and high-melting TAG fractions, whereas bulk fat exhibits broad, overlapping events characteristic of co-melting in a continuous fat phase [34]. When dispersed as micrometer-scale droplets and immobilized within a protein network, milk fat tends to exhibit greater proportions of the β polymorph rather than the β' form typically observed in bulk fat [34,37]. A study by Ramel et al. demonstrated that the shift toward the β form is not dictated by protein chemistry or templating effects, since different protein matrices result in comparable β/β' ratios [34]. Instead, the decisive factor appears to be the physical embedding of fat droplets within a solid matrix, which imposes spatial constraints that favor crystallization into thermodynamically more stable polymorphs [34]. These crystalline states remain stable during refrigerated storage, indicating that once β forms under confinement, further polymorphic transitions are unlikely under cheese-relevant conditions. Collectively, these findings highlight that controlling milk fat polymorphism through processing conditions and matrix confinement is critical for tailoring cheese microstructure, rheological behavior, texture, and melting characteristics.

3.2. Fatty Acid Composition and Functional Implications

Fatty acids are classified as saturated fatty acids (SFAs), which contain no carbon–carbon double bonds, and unsaturated fatty acids (UFAs), which contain one or more double bonds; UFAs include monounsaturated fatty acids (MUFAs), with one double bond, and polyunsaturated fatty acids (PUFAs), with two or more double bonds [45,46].

Milk fat is recognized as one of the most complex natural lipids, with its TAGs incorporating more than 400 individual fatty acids [47]. Approximately 70% of the total fatty acids are saturated, with palmitic acid (C16:0) being the dominant species, contributing

about 30% by weight. Oleic acid (C18:1) represents nearly 20%, while both stearic (C18:0) and myristic acids (C14:0) each account for close to 11% [47,48].

Cheese texture is strongly influenced by the fatty acid composition, particularly the ratio of saturated to unsaturated fatty acids. SFA, especially palmitic and stearic acids, have high melting points and contribute to firmer, denser textures, whereas UFA are associated with softer, creamier, and more elastic structures due to their lower melting points [7]. The higher chain flexibility of UFA restricts molecular packing and nucleation, leading to lower melting crystals with weaker structure, while reducing the activation energy for the transformation of unsaturated TAGs into more stable crystalline forms and thereby influencing the structural stability of the fat matrix [49]. Replacing milk fat with full-fat canola oil in Cheddar cheese analogs decreased hardness significantly compared to the control, highlighting the influence of unsaturated lipid incorporation on texture [50]. Sanders et al. further reported that plant-based cheese hardness increased with higher proportions of coconut oil while varying the ratio of coconut oil (rich in SFA) to sunflower oil (rich in UFA) [51]. Substituting milk fat with sources containing different ratios of saturated/unsaturated fatty acids has a clear impact on cheese hardness, while reported changes in other textural attributes, including chewiness, springiness, and cohesiveness, vary among studies [13,52,53].

Beyond unsaturation level, fatty acid chain length also affects cheese texture through its influence on melting and crystallization [54]. Short- and medium-chain fatty acids soften the fat phase earlier, whereas long-chain SFA form more stable crystals that increase firmness and reduce meltability [54]. In practice, cheese functionality results from the combined effects of fat source, fatty acid profile, and total fat content, which control fat crystallization and fat–protein matrix structure. Accordingly, higher UFA enhances meltability but may increase oil separation, whereas long-chain SFA reduces meltability and promotes firmer structures [54]. Fat composition changes and associated texture characteristics in some cheeses are presented in Table 1.

Table 1. Fat composition changes and associated texture characteristics in cheeses.

Type of Cheese	Modification Approach	Change in Fat Compositions	Main Texture Changes in Cheese	Ref.
Cantal-type cheese	Dietary modification	Higher UFA	Less firm and more elastic	[7]
Fresh soft rennet cheese	Canola oil replacement	Higher UFA	No significant changes in hardness, adhesiveness, springiness, cohesiveness	[55]
Fresh Pecorino cheese	Dietary modification	Higher UFA Lower SFA	Higher friability	[56]
Processed cheese	Vegetable fat replacement	Higher medium-chain SFA	Softer	[54]
Hard cooked cheese	Dietary modification	Higher UFA	Less firm and elastic	[57]

3.3. Fat–Protein Interaction

Cheese structure can be described as a continuous, gel-like protein matrix, in which fat globules are embedded and dispersed [17]. Milk fat functions as both an integral filler and a structural modifier, depending on factors such as globule size, distribution, and emulsification [6,9].

Fat globule size significantly affects cheese texture by altering the microstructure and mechanical continuity of the protein matrix [18]. Native milk fat globules, typically ranging from 1.5 to 8 μm , can be reduced to submicron bimodal populations distributed approx-

imately 0.04–2 μm , thereby increasing the interfacial surface area available for protein adsorption [58]. Both excessively small and large fat globules can weaken the structural stability of rennet-induced gels through different mechanisms [18,59]. Smaller, finely dispersed fat globules increase micro-discontinuities and water-binding capacity within the casein matrix, thereby contributing to excessive hydration and reduced firmness [18]. In contrast, larger fat globules act as structural disruptors that generate fewer but larger weak points within the protein network. When sufficiently large, fat globules act as physical barriers that constrain casein rearrangement during gelation, resulting in the development of a thicker but less interconnected protein network, with smaller globules becoming immobilized within the network pores [18,59]. Their presence disrupts casein connectivity within the gel matrix, resulting in a weaker and less cohesive network [18,59].

Smaller native fat globules promoted earlier aggregation and structural development during rennet coagulation despite exhibiting similar CMP release rates to larger globules, indicating that globule size had limited influence on the initial stage of κ -casein hydrolysis but affected subsequent organization of the casein network [18]. The increased surface area and dispersion of small fat globules reduced the effective free space available for casein micelles within the developing gel matrix. As a result, structural development occurs more rapidly, resulting in shorter gelation and set-to-cut times and firmer curds with higher storage modulus [18]. In contrast, the greater coalescence tendency of larger fat globules generated fat domains exceeding gel pore dimensions, disrupted local casein strand formation, and weakened matrix continuity and rheological stability [18]. Since curd firmness strongly influences cheese composition, texture, moisture retention, and ripening behavior, variations in fat globule size and coalescence may subsequently affect the quality and ripening characteristics of both fresh and ripened cheese systems [60]. The extent of globule coalescence is further enhanced during milk handling and curd heating due to partial disruption of the milk fat globule membrane (MFGM) and reduced spatial separation between fat globules during gel formation [61].

Homogenization further intensifies these fat–protein interactions through substantial interfacial restructuring. High-pressure treatments generate turbulence, shear, and cavitation forces that reduce globule size while partially disrupting the native MFGM, thereby exposing lipid surfaces for adsorption of casein and whey proteins [62]. Michalski et al. demonstrated that homogenized globules significantly increased gel modulus (G') only when protein coverage exceeded a critical threshold of approximately 40% of the globule surface area [62]. Below this threshold, partially damaged globules remained predominantly inert because interfacial protein density was insufficient to establish effective connectivity with the surrounding casein matrix [62]. Above this threshold, homogenized globules acted as structure-promoting particles that reinforced protein network interconnectivity and rheological strength [62]. Similar behavior has been reported in Mozzarella cheese, in which homogenization (2.6 Mpa, 50 °C) reduced fat globule cross-sectional area from 23.3 to 8.8 μm^2 and decreased free oil formation from 37.8% to 11.7% of total fat while simultaneously increasing cheese viscosity [8]. Smaller homogenized globules remained more effectively embedded within the protein matrix, whereas larger globules promoted fat pooling and structural discontinuities within the gel network [8].

In addition to their size, the surface composition of fat globules also influences their interaction with the casein matrix. During homogenization, milk fat globules are disrupted into smaller droplets under the combined effects of turbulence, shear, and cavitation, thereby increasing interfacial surface area and altering the composition of the native milk fat globule membrane [63,64]. As a result, the MFGM can no longer fully cover all fat droplets, allowing casein and whey proteins from the aqueous phase to adsorb onto the exposed surfaces and form mixed interfacial layers that behave similarly to casein micelles [65–67].

This alteration changes the role of milk-fat particles from passive fillers in the casein gel network to active fillers that interact with the casein matrix, thereby promoting closer fat–protein linkage and improving fat dispersion within the gel [67,68]. Consequently, the overall network volume increases, forming a more continuous structure that enhances moisture retention and higher yield [67,69]. In addition, the higher number of casein–fat interactions can weaken the matrix, leading to reduced mechanical stability [65]. As a result, cheeses made from homogenized milk exhibit a softer texture, reduced stretchability, and lower meltability compared with those produced from non-homogenized milk [65,70].

Variations in fat content substantially alter the balance between the fat and protein phases in cheese, thereby influencing network compactness and textural behavior. Removing fat lowers the fat-to-protein ratio, which increases the relative proportion of protein in the gel phase [71,72]. The protein strands then pack more closely, forming a denser and more continuous network that enhances gel elasticity and firmness [72]. When fat content decreases without a corresponding rise in moisture, the higher protein concentration further strengthens protein–protein associations, producing a tighter and less deformable matrix [72,73]. Low-fat cheeses generally exhibit greater hardness, fracture stress, and Young’s modulus than full-fat counterparts, even though the latter contain higher dry matter [74]. This contrast is attributed to the higher protein-to-fat ratio in low-fat systems, where the continuous protein phase dominates the structure [72,74,75]. In contrast, increasing fat content introduces more dispersed globules that are entrapped within the protein network [76]. The incorporation of these globules interrupts direct protein–protein linkages and promotes the formation of a more open, sponge-like protein structure [17,76]. Such microstructural openness, characteristic of full-fat cheeses, facilitates plasticization and deformation under stress, resulting in softer and more spreadable textures [17,76]. Collectively, cheese firmness is inversely related to the amount of fat present and directly related to protein concentration within the gel matrix.

Fat also has a critical functional contribution during heating due to the distinct thermal responses of the fat and protein phases. Milk fat undergoes melting over a broad range (0–40 °C), whereas the protein network mainly undergoes progressive thermal softening between 30 and 70 °C [77]. The transition of milk fat into a liquid phase at relatively low temperatures promotes mobility within the cheese matrix, reduces casein–casein interactions, lowers resistance to deformation, and facilitates viscoelastic [77]. By contrast, reduced-fat cheeses lack sufficient molten fat during heating, resulting in a densely cross-linked protein network that softens without transitioning to a flowing state and thus exhibits hard, brittle, and weakly melting behavior [77]. Thus, fat in cheese functions through a multi-level mechanism, including microstructure, interfacial composition, and thermal behavior, that defines the mechanical and melting response of the matrix. Understanding this mechanism provides the basis for evaluating functional equivalence in alternative lipid systems.

4. Role of Dairy Fat in Flavor Development in Cheese

4.1. Framework of Cheese Flavor Development Influenced by Milk Fat

Cheese quality is determined by a combination of flavor, rheological properties and external appearance. Depending on the type of cheese, these factors contribute at varying levels of importance. Among them, flavor is a key sensory attribute influencing consumer preference and acceptance [78]. Cheese flavor arises from complex interactions among aroma, taste, and oral sensations, in which aroma is mainly associated with volatile compounds, whereas taste is primarily related to non-volatile components [79]. While some cheeses are consumed fresh, others undergo ripening processes that substantially contribute to the development of more complex flavor profiles [80–83].

In general, cheese ripening involves four major biochemical pathways, including glycolysis, proteolysis, lipolysis, and secondary interactions among their reaction products [81,83]. During ripening, enzymatic and microbial transformations generate a wide range of volatile and non-volatile compounds responsible for cheese aroma and taste [83]. These reactions are primarily mediated by enzymes derived from starter cultures, endogenous enzymes, and, in some cheese varieties, yeasts and molds [84–86]. Non-enzymatic reaction, including lipid oxidation and Maillard reactions, may also contribute to flavor formation to a lesser extent [79,87]. However, the relative abundance and balance of volatile compounds collectively shape the characteristic flavor profiles of different cheese varieties and products from different manufacturers [78,80,88].

Milk fat acts not only as a source of aroma precursors but also as a structural phase influencing flavor retention, release, and perception [80,83]. Balanced flavor perception has been positively associated with fat concentration, suggesting that milk fat contributes to smoother and more integrated flavor profiles in cheese [89]. This observation is consistent with the component balance theory, which proposes that characteristic cheese flavor depends not only on individual compounds but also on the balance among different flavor notes [80]. For a given fat content, both the type and physicochemical state of fat influence flavor directly and indirectly through lipolysis and interfacial interactions during ripening [80]. Balanced flavor perception has been positively associated with fat concentration, supporting the role of milk fat in generating mellow, smooth, and integrated flavor characteristics in cheese [89].

The importance of milk fat is further highlighted in reduced-fat and fat-replaced cheeses, where the absence or substitution of milk fat frequently results in incomplete or atypical flavor development. Therefore, understanding the mechanistic role of milk fat in cheese flavor development is essential for designing successful fat-reduced and fat-replaced cheese systems [80,83].

4.2. Milk Fat as a Primary Source of Flavor Precursors Through Lipolysis

Lipolysis is one of the major biochemical pathways contributing to cheese flavor development during ripening. The initial step in lipid degradation involves triglyceride hydrolysis, which releases free fatty acids that subsequently serve as precursors for numerous volatile compounds associated with characteristic cheese aroma [80,90,91]. Lipolysis is mediated by lipases originating from milk, residual coagulants, starter and non-starter microorganisms, secondary microbiota, and exogenous enzymes [80]. Two major classes of lipid-degrading enzymes are involved during cheese ripening: lipases, which hydrolyze triglycerides, and esterases, which primarily act on water-soluble ester substrates [80,83,92,93]. Most lipolytic enzymes preferentially hydrolyze fatty acids esterified at the sn-1 and sn-3 positions of milk triglycerides, whereas hydrolysis at the sn-2 position remains limited. The extent of lipolysis, commonly expressed as Acid Degree Value (ADV), generally increases progressively throughout maturation [93].

Lipid degradation in blue cheese is mainly attributed to the extracellular lipase produced by *Penicillium roqueforti*, which preferentially releases higher amounts of long-chain fatty acids (LCFA) than short-chain fatty acids (SCFA) [94]. In contrast, milk lipoprotein lipase exhibits greater activity toward short-chain fatty acids, particularly in raw milk cheeses [94]. The lipolytic activity of *P. roqueforti* may contribute to the formation of butanoic and hexanoic acids, which are associated with characteristic moldy flavors in blue cheese [89]. Generally, cheeses characterized by high levels of FFAs are associated with strongly lipolytic secondary microflora, the use of rennet paste, or extended ripening periods [80]. During ripening, the proportion of LCFA relative to total FFAs tends to increase during the early stages and subsequently stabilizes, whereas the proportion of

medium-chain fatty acids (MCFA) decreases and SCFA remain relatively constant after the first few months of maturation [93,95,96]. Although LCFA quantitatively predominate in many cheeses, including blue and white-mold cheeses, their contribution to flavor is relatively limited because of their high perception thresholds and retention within the fat matrix [79,83,97]. In contrast, SCFA and MCFA exhibit considerably lower perception thresholds and therefore contribute more significantly to cheese flavor [79,83,97]. Odor threshold values of FFAs range widely from 0.00245 to 15,000 ppm, with most SCFA and MCFA exhibiting threshold values below 15 ppm [97].

Furthermore, the sensory impact of FFAs is strongly influenced by cheese matrix composition, pH, and the polarity of the surrounding medium, since odor and flavor potentials are generally lower in oily media than in aqueous solutions [79,80]. Consequently, short- and medium-chain FFAs exert a stronger influence on cheese flavor than LCFA, which are often retained within the fat matrix during extraction [83,91,98].

Depending on their concentration, volatile FFAs may contribute desirable cheesy, pungent, and moldy notes or, when excessively accumulated, result in rancid off-flavors [80,83,99,100]. In mold-ripened cheeses, however, extensive lipolysis does not necessarily lead to rancidity due to the neutralization of fatty acids [83]. In blue cheese and white-mold cheeses, although LCFA predominate quantitatively, SCFA and MCFA remain the principal contributors to characteristic flavor development in mold-ripened cheeses [83,93,95,96].

However, the extent of lipolysis varies substantially among cheese varieties. Extensive lipolysis is particularly associated with blue cheeses, smear-ripened cheeses, and hard Italian cheeses, where lipid-derived volatiles are major contributors to flavor development [80,83]. In contrast, cheeses such as Cheddar, Mozzarella, and Gouda generally undergo less extensive lipolysis during ripening [80,83]. While lipolysis usually involves less than 2% of total triglycerides in cheeses such as Cheddar or Gouda, it may reach 5–20% in mold-ripened cheeses, resulting in substantial accumulation of FFAs and secondary volatile compounds [80,83]. Importantly, lipolysis does not occur independently but interacts dynamically with proteolysis, amino acid catabolism, and microbial metabolism throughout ripening, collectively shaping the complexity and diversity of cheese flavor profiles [80,83]. Major aroma compounds in cheese associated with lipolysis are summarized in Table 2.

These observations also highlight one of the major limitations of plant-based cheese alternatives. Plant-derived fats often contain substantially different fatty acid compositions and triglyceride structures compared with milk fat, resulting in reduced availability of characteristic dairy flavor precursors. Consequently, plant-based cheese alternatives frequently exhibit limited lipid-derived flavor development and often require external flavor additives to mimic cheese-like flavors [15,101–103].

4.3. Secondary Aroma Compounds Derived from Milk Fat Metabolism

In cheese, FFAs also serve as substrates for the formation of a wide range of secondary aroma compounds, including methyl ketones, alcohols, lactones, aldehydes, and esters [81,93,98,104]. These compounds exhibit a wide range of sensory attributes, from fruity and sweet notes to pungent, mold-ripened, and sulfurous aromas [105,106]. Secondary aroma compounds in cheese are summarized in Table 2, while fat-associated flavor characteristics in cheese varieties are presented in Table 3.

Among secondary lipid-derived volatiles, methyl ketones are major contributors to the characteristic aroma of blue-vein cheese and are generated through the β -oxidation of fatty acids by *P. roqueforti*. A positive correlation has been reported between FFA concentration and methyl ketone formation, whereas high salt concentrations may suppress mold growth, retard lipolysis, and reduce methyl ketone production [83,99,105,107,108]. Reduction of

methyl ketones leads to secondary alcohols that contribute additional sweet and alcoholic notes to cheese aroma [91,104]. Compounds such as diacetyl (2,3-butanedione) contribute buttery and nutty notes, while other ketones are associated with spicy or faintly smoky aromas characteristic of blue cheeses [109].

Esterification between fatty acids and alcohols produces esters that contribute fruity and sweet aromatics important for the desirable aroma of many cheeses. Some lactic acid bacteria can synthesize esters through esterase activity. Alcohols may originate directly from forage, particularly when animals are fed silage [110]. Lactones, formed through intramolecular esterification of hydroxy fatty acids, may contribute to overall cheese flavor despite having low flavor thresholds and lacking characteristic cheese-like aromas [80,83]. Some thioester compounds are produced through the reaction of free fatty acids with sulfhydryl groups, which have a garlicky, sulfur-like, or eggy flavor [80,99,111].

Cheeses produced from raw milk often exhibit more desirable flavor profiles, as raw milk contains higher levels of FFAs, supports greater ester formation, and retains naturally occurring lipolytic LAB [92]. In addition, depending on plant-based feed, especially dicotyledonous forage, the milk may contain lactones or terpenoids that critically affect final cheese aroma [99,110].

Table 2. Major aroma compounds associated with cheese flavor [97,106,112,113].

Group	Name	Odor Descriptor	Odor Threshold in Water	Primary Catabolism Pathway
Acid carboxylic	Acetic acid **	Acetic, sour	22 ppm/7 ppm (in butter)	Lactose fermentation
	Butanoic acid *	Sharp, cheese, sweaty, putrid, sour	0.6–6.8 ppm	Lipolysis
	Pentanoic acid *	Putrid, sweaty, rancid	1.1–6.5 ppm	
	Hexanoic acid *	Sickening, sweaty, rancid, sour, sharp, pungent, cheesy, fatty	1–15 ppm	
	3-methyl butanoic acid **	Rancid, cheese, sweaty, putrid	0.07–1 ppm	Amino acid catabolism
	Octanoic acid *	Unpleasant, oily, fatty odor, rancid taste	3–5.8 ppm/350 ppm (in butter)	Lipolysis
	Decanoic acid *	Fatty, unpleasant, rancid, citrus	2.2–10 ppm/200 ppm (in butter)	
Ester	Ethyl butanoate *	Fruity, apple-like, banana, pineapple	0.13–1 ppb	Esterification: butanoic acid + ethanol
	Ethyl hexanoate *	Pineapple, ether	0.3–5 ppb	Hexanoic acid + ethanol.
	3-Methylbutyl acetate *	Fruity, banana	2–5 ppb	Acetic acid + 3-methylbutanol
	Isobutyl butanoate *	Fruity	9.4 ppb	Butanoic acid + isobutanol
	Ethyl octanoate *	Fruity, banana, apple-like	5–5.8 ppb	Octanoic acid + ethanol.
	Phenyl ethyl acetate **	Fruity	19–480 ppb	Acetic acid + phenyl ethanol
	Ethyl decanoate *	Brandy, oily, fruity, grape-like	5–23 ppb	Decanoic acid + ethanol
Ketones	3-Hydroxy-2-butanone (Acetoin) **	Buttery	140 ppb	Citrate metabolism
	2-Pentanone *	Sweet, fruity, cheesy	1.6–4 ppm	β -oxidation of fatty acids
	2-Hexanone *	Blue cheese	40–81 ppb	
	2-Heptanone *	Blue cheese, spicy, cinnamon	21–140 ppb	
	2-Nonanone *	Fruity, floral	5–41 ppb	

Table 2. Cont.

Group	Name	Odor Descriptor	Odor Threshold in Water	Primary Catabolism Pathway
Alcohols	Ethanol **	Alcohol, mild	3.5–2000 ppm	Glycolysis/Fermentation
	2-Heptanol *	Earthy, oily, sweetish	300–500 ppb	Reduction of methyl ketone
	1-Octen-3-ol *	Mushroom	1–10 ppb	Oxidation of fatty acids
	2-Nonanol *	Fatty, melon, mild green	85–180 ppb	Reduction of methyl ketone
	3-Methyl-1-butanol **	Fusel oil, whiskey	250–300 ppb	Amino acid catabolism
	2-Methyl-1-butanol **	Fruity, alcohol	300 ppb	
	Phenyl ethanol **	Rose flower	750 ppb	
	3-Methyl butanal **	Green, malty	1–2 ppb	
	Acetaldehyde **	Ethereal, pungent, green	1.5 ppb	
	Phenyl acetaldehyde **	Floral, broom	4–6.3 ppb	
Lactones	3-Methyl thiopropanal (methional) **	Boiled potato	0.2–1 ppb	Amino acid catabolism
	δ - decalactone *	Creamy, coconut, peach, milk	100 ppb	From hydroxy fatty acids
	δ - dodecalactone *	Fruity, coconut, peach, pear	45 ppb	
	γ -nonalactone *	Coconut, almond, anise	30 ppb	
	γ -decalactone *	Fruity, peach	1–11 ppb	
Terpen	Styrene **	Plastic	3.6–730 ppb	Carry-over from feed
	Limonene **	Fruity, lemon	4–1000 ppb	
Maillard-derived compounds	2,3-Dimethyl pyrazine **	Roasted nuts, coffee, peanut, butter	400–2500 ppb	Maillard reaction
	Furaneol **	Burnt sugar, caramel notes	0.03–200 ppb	Carbohydrate metabolism
Anisole	4-Methylanisole **	Gorgonzola cheese	160 ppb	Metabolism of phenolic compounds

* Directly formed through lipid metabolism or secondary conversion of lipid-derived precursors; ** primarily associated with non-lipid metabolic pathways.

Table 3. Fat-associated compounds and flavor characteristics in different cheeses.

Cheese Type	Key Lipid-Derived Compounds	Major Secondary Volatiles from Fat	Characteristic Flavor Profile	Refs.
Gorgonzola	Butanoic acid, Hexanoic acid, Octanoic acid, Decanoic acid	1. Ketones: 2-heptanone, 2-nonanone 2. Alcohols: 1-octen-3-ol, heptan-2-ol, nonan-2-ol. 3. Ester: ethyl hexanoate, ethyl butanoate	1. Piquant Gorgonzola: salty, moldy/ammonia, pungent, and grainy characteristics; 2. Sweet Gorgonzola: sweet, creamy, and floral characteristics	[97,109,112,114,115]
Stilton	Butanoic acid, Hexanoic acid, Octanoic acid, Decanoic acid, 3-methylbutanoic acid	1. Ketones: 2-heptanone, 2-nonanone 2. Alcohols: heptan-2-ol, nonan-2-ol 3. Ester: ethyl butanoate	Creamy, moldy, slightly sharp, and metallic flavor characteristics	[88,89]
Camembert	Butanoic acid, Hexanoic acid, Octanoic acid, Lauric acid, Palmitic acid, Oleic acid, Hexanoic acid	1. Ketones: 2-heptanone, 2-nonanone, 2-undecanone 2. Alcohols: 1-octen-3-ol 3. Ester: ethyl octanoate, ethyl butanoate and ethyl hexanoate	1. Young cheese: sour and weak aroma; 2. Moderately ripened cheese: mushroom-like, buttery, soft, and elastic characteristics; 3. Over-ripened cheese: ammonia odor	[91,116,117]
Full fat Cheddar	Butanoic acid, Pentanoic acid, Hexanoic acid, Octanoic acid, Decanoic acid	1. Ketones: 2,3-butanedione, 2-heptanone 2. Ester: ethyl butyrate, ethyl caproate 3. Lactones: δ -decalactone, γ -decalactone	1. Long-ripened cheese: fruity and sulfur notes 2. Younger cheese: spicy and brothy flavor	[87,101,118–120]
Low fat Cheddar	Butanoic acid, Hexanoic acid	1. Lactones: *	Bitter, rosy, burnt, and weaker creamy/fatty	[120,121]

* Not specified.

4.4. Milk Fat as a Matrix Regulating Aroma Retention and Sensory Perception

In cheese, fat functions as a solvent and retention medium for hydrophobic volatiles, regulating their release through interactions with moisture and thereby creating a complex flavor profile.

Although cheeses contain a broad range of odor-active volatile compounds, 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 [91]. Changes in fat content can substantially alter the physical chemistry of the cheese matrix, thereby affecting the partition coefficients and release behavior of volatile compounds [83]. In addition, flavor perception is influenced by matrix breakdown and oral processing during consumption. Saltiness perception in blue cheese depends on salt diffusion and the contact area between the cheese matrix and saliva, both of which are affected by cheese fracture behavior and chewing energy during mastication [94]. Harder cheeses with more spherical fat globules contribute to a more stable system that can limit the diffusion of hydrophobic volatile compounds [121,122]. In a stable fat matrix, small and relatively polar molecules such as ethanol, dimethyl disulfide, and acetaldehyde volatilize and diffuse more easily, whereas less polar, higher-molecular-weight molecules such as methyl butanal, hexanal, and heptanal are retained more effectively [121,122]. The interaction between fat and moisture also determines whether the cheese matrix is less or more polar [121]. When fat content decreases and moisture increases, the matrix shifts dramatically toward a more polar state [121]. This fundamental change not only reduces the ability to retain creamy flavor notes but also promotes new biochemical reactions, resulting in the abnormal accumulation of off-flavor compounds, such as furanones with burnt or rosy notes, as well as the development of intense bitterness, disrupting the inherent flavor balance [121].

Additionally, milk fat acts as a sensory modulator by masking or softening undesirable tastes such as bitterness derived from peptides, partly through limiting interactions between bitter compounds and taste receptors. Reduction of milk fat often results in less balanced flavor perception and increased susceptibility to off-notes [120,121]. Milk fat also contributes to oral lubrication and aroma release behavior during consumption, thereby enhancing creaminess, smoothness, mouth coating, flavor persistence, and overall sensory balance [123,124]. Lipid compounds such as oleic acid may further reduce bitterness perception and improve mouthfeel characteristics [123,124].

4.5. Indirect Modulation of Proteolysis- and Carbohydrate-Derived Flavor by Milk Fat

The most critical biochemical process controlling flavor and texture development in hard and semi-hard cheeses is protein hydrolysis [91]. Proteolysis begins when milk caseins are cleaved into peptides and amino acids by enzymes originating from rennet and bacteria [81,99]. Small peptides and amino acids are primarily responsible for generating the basic background taste attributes (umami, sweetness, bitterness, and saltiness), upon which characteristic cheese flavors are built through subsequent enzymatic or chemical transformations [91]. Free amino acids (FAAs) are strongly associated with the volatile compounds of cheese because they serve as precursors for numerous aroma-active volatiles, including amines, carboxylic acids, thiols, esters, alcohols, aldehydes, and thioesters. Arginine (Arg) is associated with bitterness, whereas Proline (Pro), Serine (Ser), and Asparagine (Asn) contribute to sweetness [91,93]. The catabolic pathways of branched-chain and aromatic amino acids proceed through transamination and decarboxylation reactions, yielding aldehydes (green, malty, or potato-like aromas), alcohols (sweet or floral notes), and carboxylic acids or esters that often exhibit fruity, rancid, or pungent aromas of varying intensities [82,93,99]. In addition, the formation of intermediate methanethiol derived from methionine leads to

sulfur-containing compounds such as dimethyl sulfide (DMS), dimethyl disulfide (DMS), which imparts garlic-like notes, and dimethyl trisulfide (DMTS), characteristic of overripe cheese [81,91,99,110]. The transformation of tryptophan or phenylalanine in many hard and soft cheeses results in the formation of benzaldehyde, which contributes a distinct bitter almond aroma [99]. Aldehydes are formed from amino acids via transamination or Strecker degradation and are short-lived in cheese, as they are rapidly converted to alcohols or acids [118]. The ammonia-like note found in Gorgonzola PDO is mainly linked to 4-methyl-2-pentanol, methyl hexanoate, dimethyl sulfone, and methanethiol produced during amino acid catabolism [114]. The concentrations of methionine, leucine, and glutamic acid are often regarded as indicators of the extent of proteolysis in cheese [99].

Although proteolysis is not directly linked to lipid degradation, the sensory expression of proteolysis-derived compounds is strongly influenced by milk fat. Fat modulates the perception of these compounds by masking bitterness, regulating release kinetics, and altering matrix polarity. As a result, differences in fat content are associated with changes in peptide profiles, bitterness perception, and overall flavor balance [121,123,125]. Therefore, bitterness is less perceptible in high-fat cheese than in low-fat cheese [121,123,125].

Similarly, while proteolysis establishes the foundational flavor of cheese, carbohydrates and citrate metabolism, though secondary, contribute to refining the overall flavor profile. Lactose is rapidly converted into lactate, forming a fundamental acidic note, while citrate metabolism in certain cheese types generates diacetyl and CO₂, enhancing sharpness and adding complexity to the aroma [126]. The perception of these metabolites is also regulated by the fat-moisture balance of the cheese matrix [80–82,104].

Fat, the protein matrix, moisture, and hydrocolloids are the main factors influencing the structure and flavor perception of processed cheese. High milk fat combined with moderate moisture enhances flavor perception by promoting the release of aroma compounds and improving oral lubrication, thereby strengthening overall aroma perception [54]. In contrast, in a processed cheese system, low fat and protein combined with high carbohydrate content generally reduce flavor intensity and significantly alter aroma release kinetic [54].

5. Mechanistic Implications for Fat Replacement in Cheese Systems

The multifunctional roles of milk fat described in the previous sections provide important insight into why reducing/replacing dairy fat in cheese remains challenging. In cheese matrices, milk fat simultaneously contributes to structural organization, flavor precursor generation, and aroma perception. These functions arise from interconnected physico-chemical mechanisms, including lipid crystallization behavior, interfacial interactions with proteins, lipolysis, and lipid-mediated aroma retention. Given these combined functions, modifying or reducing fat while maintaining desirable properties remains a major challenge in cheese systems. Accordingly, current strategies aim to replicate or modulate fat functionality while preserving product qualities. In practice, dairy fat substitutes appear in various forms (vegetable oils, waxes, hydrocolloids, whey protein/casein derivatives, ...) and have been applied in dairy products to provide the sensory and functional attributes normally associated with fat [12,127]. As a result, many current fat replacement strategies attempt to reproduce specific functional aspects of milk fat rather than replicating its native structure and functional behavior. Several technological approaches have therefore been explored to address different mechanistic roles of milk fat within cheese systems.

5.1. Replicating Lipid Crystallization and Melting Behavior

Both milk fat and plant-derived fats can crystallize into three polymorphic forms: α , β' , and β [21,35,128]. However, the simpler TAG composition of many plant-derived fats

often favors β crystal formation, which can result in larger crystals and grainy texture [128]. To address this challenge, structured lipid systems have been explored to modify the physical behavior of liquid vegetable oils. Oleogelation, for example, converts liquid oils into semi-solid systems through the incorporation of an oleogelator (Figure 2). During this process, oleogelator molecules (commonly phytosterols, monoglycerides, fatty acid, wax) crystallize and self-assemble within the oil phase to form a three-dimensional network, which is stabilized by intermolecular interactions such as hydrogen bonding and van der Waals forces [129,130]. As the crystals grow and aggregate during cooling, they form clusters that develop into a continuous network. This network immobilizes the liquid oil within its structure and restricts oil mobility. Through this mechanism, oleogels can increase firmness and structural stability, allowing liquid oils to behave more like semi-solid fats [131,132]. Noon et al. showed that oleogelation significantly reduced saturated fat content in vegan cheese (from 28% to as low as 2%), while generally improving meltability; however, the functional properties of the oleogels were not consistently observed in the final cheese matrix, and oxidative stability was often lower than in the control systems [133]. Also, a study by Moon et al. demonstrated that incorporating oleogels into dairy-free cheese formulations reduced saturated fat content from 45.70% to 5.20%, while maintaining meltability comparable to the palm-oil control at oleogel levels of 3% and 6% [53].

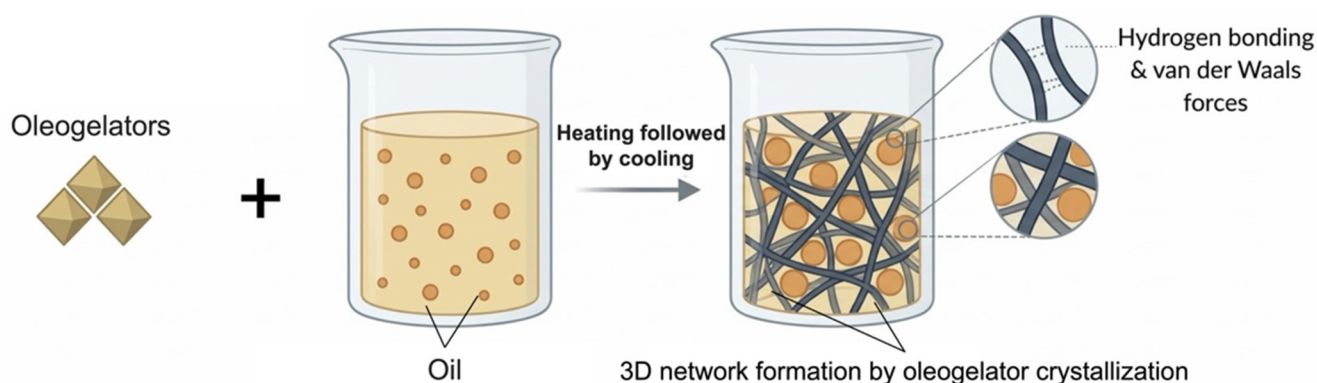


Figure 2. Oleogelation: crystallization and network formation.

Another strategy involves modifying lipid functionality through interesterification, a process that rearranges fatty acids on the glycerol backbone of TAG molecules. This rearrangement generates new TAG combinations while largely preserving the overall fatty acid composition, thereby altering melting behavior and SFC through changes in TAG distribution [16]. Interesterification reactions can occur through several related pathways, including alcoholysis, acidolysis and glycerolysis, depending on the co-reactant involved (Figure 3) [134,135]. These reactions can be carried out using either chemical or enzymatic catalysis [16,134,136]. Chemical interesterification typically uses alkaline catalysts under elevated temperatures [137], whereas enzymatic interesterification uses lipases that allow more selective rearrangement of fatty acids within TAG molecules [16,138].

5.2. Modifying Interfacial Interactions Within the Protein Matrix

The interfacial composition of fat droplets determines their interactions with the surrounding casein network. Experimental studies have shown that disruption or absence of the native MFGM reduces protein adsorption at the droplet surface, weakening droplet–protein interactions and reducing structural stability in cheese systems [62,139]. Several strategies have been developed to engineer the oil–water interface so that dispersed lipid droplets interact more effectively with the surrounding protein network. The following

section discusses several potential mechanisms associated with these approaches and their promising applications in cheese systems.

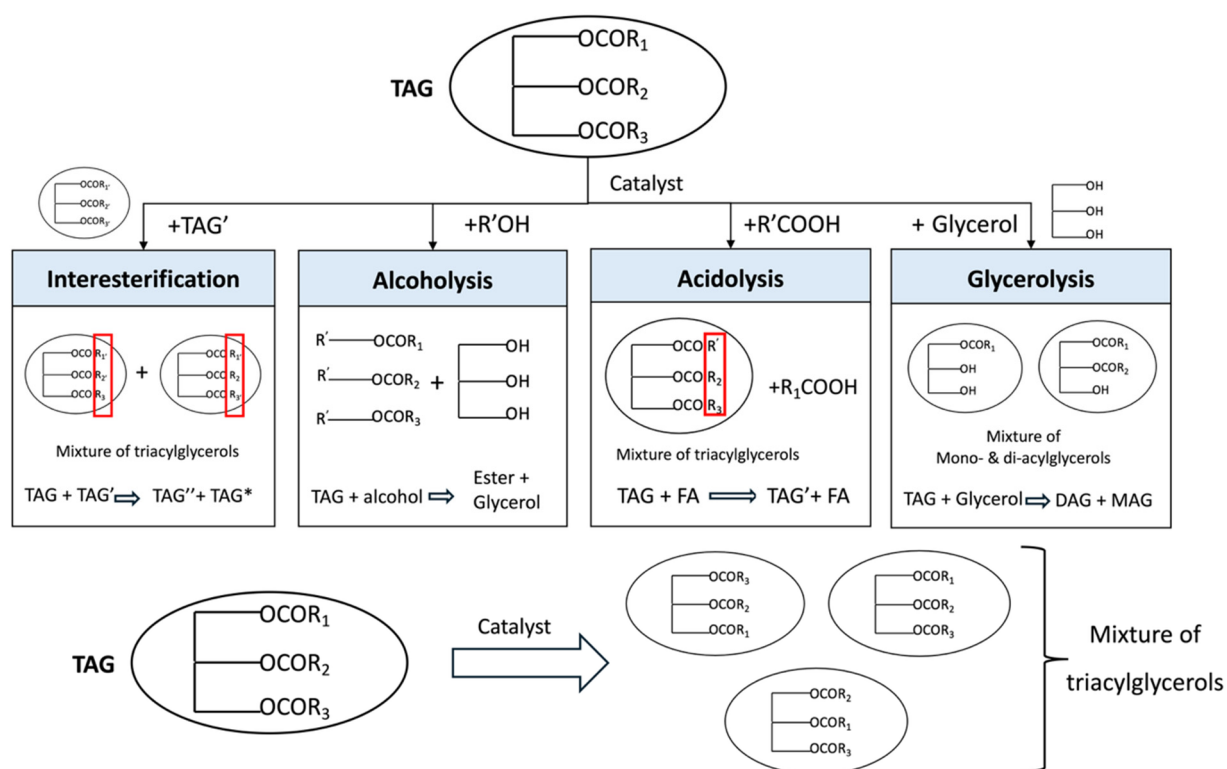


Figure 3. Mechanisms of interesterification in lipid.

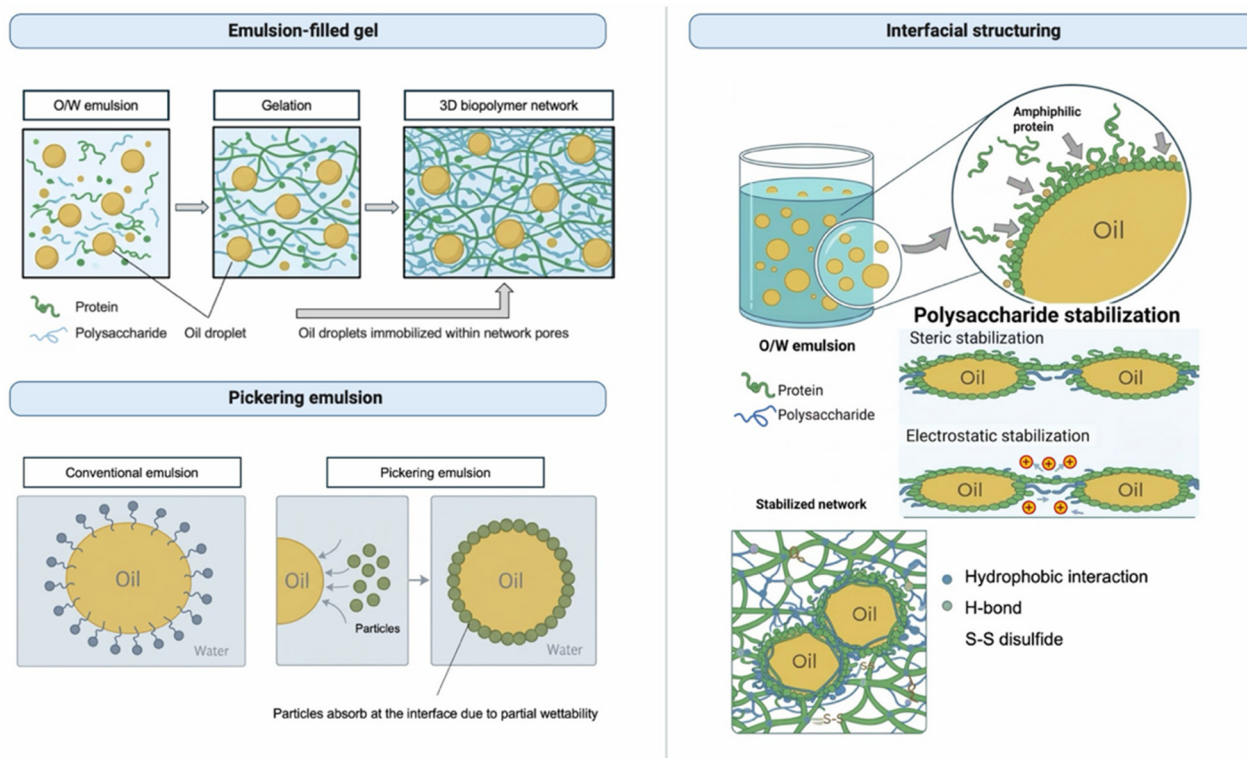


Figure 4. Potential strategies for modifying interfacial interactions within the protein matrix.

(i) One strategy involves interfacial structuring, where proteins or surface-active biopolymers are used to stabilize lipid droplets and promote interactions with the sur-

rounding matrix (Figure 4). Proteins are natural amphiphilic molecules with interfacial activity that readily adsorb at oil–water interfaces [140,141]. Their adsorption reduces interfacial tension and forms viscoelastic interfacial layers that stabilize dispersed droplets against flocculation or coalescence [141]. Under appropriate conditions, these proteins may also participate in network formation through hydrophobic interactions, hydrogen bonding, or disulfide cross-linking [141,142]. In more complex systems, hybrid biopolymers containing both protein and polysaccharide segments may also assemble at the interface, where the protein component typically modulates adsorption, while the polysaccharide segments contribute additional steric or electrostatic stabilization [143–145]. As a result, protein-stabilized droplets interact more effectively with the surrounding protein network, functioning as structural elements rather than passive inclusions in cheese-like systems.

(ii) Another strategy involves network immobilization through emulsion-filled gels, where lipid droplets are dispersed within a three-dimensional network formed by gelation of the continuous phase (Figure 4) [146]. In these systems, the aqueous phase, typically composed of proteins or polysaccharides such as starch or carrageenan, undergoes gelation to form an interconnected biopolymer network [147]. This network physically entraps the dispersed lipid droplets within its pores, thereby restricting droplet mobility and limiting oil migration within the matrix [147,148]. As a result, the immobilized droplets remain uniformly distributed within the gel structure, which helps maintain microstructural homogeneity and reduce oil separation in cheese-like systems.

(iii) A third strategy involves Pickering emulsions (particle-stabilized interfaces), in which solid food-grade particles adsorb at the oil–water interface to stabilize dispersed lipid droplets (Figure 4) [149,150]. In this system, particles must exhibit partial wettability with both oil and water, allowing them to preferentially absorb at the interface where the interfacial free energy is minimized [149–151]. Because the adsorption free energy of these particles is substantially higher than that of conventional surfactants, they remain strongly associated with the interface and form a particulate layer around the droplets [150]. This interfacial layer provides an effective barrier against droplet coalescence and improves emulsion stability in complex food systems such as cheese-like matrices [152,153].

The lipid structuring approaches used to improve texture in dairy cheeses are summarized in Table 4. Collectively, these strategies aim to improve the structural integration of dispersed lipid droplets within the protein matrix, thereby enhancing matrix cohesion and reducing oil separation in cheese-like systems.

Table 4. Lipid structuring approaches for texture improvement in dairy cheese systems.

Strategy	Cheese System	Modification Approach	Functional/Textural Effect	Potential Limitations	Ref.
A. Oleogelation					
	Cream cheese	Sunflower oil oleogels replaced 50–100% milk fat	Maintained solid-like behavior, improved spreadability.	High replacement disrupted casein matrix continuity, resulting in weaker structural integrity and softer cheese textures.	[154]
	Cream cheese	RBW/EC oleogels incorporated into reduced-fat cream cheese formulations.	1. 25% fat reduction and increase in unsaturated fat. 2. RBW and EC samples showed hardness, spreadability, stickiness, fat globule size comparable to full-fat controls	1. EC lowered cheese adhesiveness and storage modulus. 2. Oleogels altered low-temperature rheological behavior (5–30 °C) compared with full-fat controls.	[155]

Table 4. Cont.

Strategy	Cheese System	Modification Approach	Functional/Textural Effect	Potential Limitations	Ref.
B. Emulsion	Processed cheese	Processed cheese formulated with 10% soybean oil oleogels structured using 0.5–1.0% RBW/SW.	1. Reduced saturated fat (20–22%) while maintaining comparable hardness, storage modulus, and meltability comparable. 2. Increasing wax concentration strengthened crystalline lipid networks and reduced oil loss to $\leq 0.7\%$	Above 70 °C, wax melting released mobile vegetable oil molecules that weakly interacted with casein, destabilizing the protein–fat network during heating.	[156]
	White-brined cheese	RF and FF cheese emulsions prepared with different dry matter (15–25%) and ES (0–3%) levels	1. Stable emulsions were obtained at 25% DM (FF) and 20–25% DM (RF) with 3% ES. 2. Increasing ES improved fat dispersion and emulsion stability. 3. Fat reduction increased apparent viscosity and pseudoplastic behavior due to higher protein content.	Fat reduction significantly increased viscosity, reducing flowability and causing difficulties during pumping and spray drying.	[157]
C. Interfacial structuring					
D. Interesterification	Processed cheese	1. WPI emulsions prepared from heat-treated 8% WPI and butter 2. WPI-pectin bilayer emulsions formed by coating WPI emulsions with 2% pectin under acidic conditions.	1. WPI-pectin bilayer emulsions improved thermal stability, reduced droplet aggregation and oil release (~10%) during storage. 2. The bilayer system increased a more uniform fat distribution and compact cheese microstructure, resulting in the higher hardness and lower melting temperature.	Heat-treated may partially disrupt protein structure, weakening interfacial stability and oil immobilization.	[158]
	Turkish white Cheese	Turkish white cheese formulated with 0–1.5% interesterified fat from palm, palm kernel, and soybean oils (melting point 22 °C)	1. Interesterified fat increased the PUFA/SFA ratio from 0.04 to 0.94. 2. Most interesterified-fat cheeses exhibited higher hardness, gumminess, and chewiness than the control cheese.	-	[159]

In dairy cheese systems, several fat-structuring strategies have demonstrated the ability to maintain acceptable sensory quality despite substantial modification of the lipid phase. Several oleogel and emulsion formulations maintain flavor acceptability comparable to conventional cream cheese [154]. Similarly, interesterified vegetable fats with increased unsaturation could be incorporated into white cheese without adverse effects on sensory acceptability, bitterness, or rancidity [159]. However, sensory performance remains highly dependent on formulation. In oleogel cream cheese systems, formulations with texture and mouthfeel comparable to full-fat controls exhibited excessively strong flavor and bitterness, indicating that rheological similarity alone is insufficient to ensure balanced sensory perception [155]. This suggests that oleogelator type, lipid composition, and matrix interactions may influence bitterness perception, flavor release, and aftertaste independently of texture recovery [154,155].

A similar trend is observed in plant-based and cheese analog systems, where the effectiveness of these strategies becomes strongly linked to their ability to reconstruct flavor precursor composition. Among current approaches, interesterification appears more effective in improving flavor quality. HOSO interesterified with SCFA could improve Swiss

cheese-like flavor profiles comparable to milk-fat controls, whereas unmodified HOSO systems showed substantially weaker flavor intensity [160]. These findings suggest that successful flavor recovery depends not only on SCFA availability but also on their structural integration into the lipid matrix, which may support more effective flavor development during ripening [160]. However, sensory response depends on SCFA concentration, as excessive SCFA incorporation increases sourness and volatile intensity, indicating that reconstruction of dairy-like flavor requires not only sufficient precursor availability but also an appropriate balance in precursor concentration [160]. Oleogelation also demonstrates potential in plant-based cheese alternatives. Oleogel-based PCA systems could produce comparable volatile compounds commonly detected in animal-based cheeses, suggesting that structured lipid systems may support cheese-like volatile development even in non-dairy matrices [161]. However, generation of cheese-associated volatiles alone is insufficient to reproduce dairy-like sensory perception [161].

Emulsion and interfacial structuring strategies have also shown potential for improving structural and sensory-related properties in both dairy cheese and cheese analog systems [162]. In processed Cheddar cheese, olive oil-whey protein isolate emulsions improve aroma, taste, texture, and overall acceptability, suggesting that emulsion structuring may support both textural and sensory quality. However, sensory performance remains strongly dependent on formulation, particularly emulsion concentration [162]. Similarly, interfacial structuring approaches using micro-biosurfactants in reduced-fat cheese analogs improve creaminess and overall sensory perception [163]. Nevertheless, further investigation is still required to better understand their influence on flavor development and sensory perception in both dairy and alternative cheese systems.

5.3. Modulating Lipid-Derived Flavor Pathway

The absence of dairy fat in cheese analogs not only alters the structural properties of the matrix but also disrupts the formation of lipid-derived flavor compounds. In conventional cheese, lipolysis of milk triglycerides generates short- and medium-chain fatty acids that serve as key precursors for characteristic aroma compounds during ripening. When dairy fat is removed or substantially reduced, the availability of these lipid-derived precursors declines, limiting the development of typical cheese-like flavor profiles.

Several strategies have therefore been explored to compensate for the loss of these lipid-derived flavor pathways. One commonly applied approach involves the incorporation of flavor-enhancing ingredients, such as nutritional yeast, salts, sugars, acidulants, and plant-derived extracts, which can improve flavor intensity and partially mimic dairy-like sensory notes [15]. However, the present review focuses primarily on strategies that compensate for the loss of lipid-derived flavor precursors associated with dairy fat.

Microbial fermentation is recently considered a powerful tool to generate cheese-like volatile compounds within the matrix. Selected lactic acid bacteria, yeasts, and molds can produce volatile compounds such as diacetyl, acetoin, and 3-methylbutanal while simultaneously reducing undesirable off-flavors (hexanal, pentanal) [101,164]. Nugroho et al. reported that heterofermentative lactic acid bacteria effectively reduced aldehydic off-flavors while enhancing the formation of important cheese-like aroma compounds such as ethyl acetate (sweet, fruity) and α -diketones (buttery, cheese-like) [165]. Similarly, Masiá et al. evaluated 24 bacterial blends composed of different starter and adjunct cultures for flavor development in plant-based cheeses. Blends containing five adjunct cultures were particularly effective in reducing off-flavors, and fermentation generated dairy-related volatile compounds such as diacetyl and 2,3-pentanedione [164].

Despite these advances, reproducing the complex pathway of lipid-derived flavor formation observed in traditional cheese remains challenging, as aroma development

depends on tightly coupled interactions between lipid composition, microbial metabolism, and matrix structure.

5.4. *Modulating Aroma Retention and Sensory Perception*

Beyond aroma formation, milk fat also influences the retention and release of volatile compounds by acting as a reservoir for hydrophobic aroma molecules within the cheese matrix. Consequently, reduction or replacement of dairy fat may alter volatile partitioning and aroma persistence in cheese systems. Encapsulation technologies have therefore been promising for flavor stability enhancement and aroma retention under these conditions.

Encapsulation technologies have been explored as a strategy to improve aroma retention in food systems by protecting volatile compounds from premature loss during processing and storage. In these systems, flavor molecules are entrapped within carrier or wall materials, typically proteins, polysaccharides, or lipids, which act as physical barriers between volatile compounds and the surrounding environment [166,167]. This approach can reduce volatilization, oxidation, and chemical degradation of aroma compounds while enabling more controlled release behavior [166]. Although encapsulated flavor systems have been widely investigated in various dairy products, including yogurt and ice cream, their application in cheese matrices remains relatively limited [167,168]. Advanced approaches such as ultrasound-assisted emulsification prior to encapsulation enhance volatile retention during spray-drying, and improve sensory acceptance by masking undesirable flavors and reducing lipid oxidation [169,170]. Encapsulation also contributed to improvements in textural properties within the cheese matrix [168]. However, several limitations still restrict the practical application of encapsulation technologies in cheese products. Selective retention of volatile compounds during encapsulation may alter the original cheese aroma profile, resulting in differences from traditional dairy fat flavor characteristics [170]. In addition, the effectiveness of encapsulation strongly depends on wall material selection, since materials such as chitosan, whey protein, cellulose derivatives, alginate, and plant gums influence microcapsule stability, release behavior, and compatibility with the cheese matrix [171]. Industrial-scale encapsulation further requires specialized equipment, controlled processing conditions, and high production costs, thereby limiting large-scale commercialization feasibility [168,170].

6. Conclusions and Future Research Perspectives

Milk fat contributes to cheese quality through interconnected structural and biochemical functions that collectively influence texture, flavor development, and sensory perception. This review highlighted the molecular, physicochemical, and biochemical roles of milk fat in shaping cheese texture and flavor characteristics. Current fat-structuring approaches demonstrated the ability to partially compensate for the multifunctional roles of milk fat in cheese systems and showed favorable effects on cheese functionality, texture, and, in some cases, sensory quality in both dairy and cheese analog products. Complementary strategies, including controlled fermentation and flavor encapsulation, also emerged as promising approaches for overcoming limitations in flavor development and aroma perception associated with fat restructuring technologies. Despite these advances, several research gaps remain, particularly regarding sensory evaluation and flavor development. Current studies mainly focus on texture and functionality, whereas the influence of fat structuring on flavor perception and sensory quality remains insufficiently explored despite the evident impact of these approaches on flavor characteristics. Future research should therefore investigate structural and sensory responses simultaneously, particularly for interesterification and interfacial structuring approaches, for improving cheese texture and functionality under conditions of fat reduction or replacement. In addition, integrating

fat-structuring technologies with complementary strategies such as controlled fermentation and flavor encapsulation may provide a more effective direction for improving both texture and dairy-like flavor perception in future cheese reformulation strategies.

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Abbreviations

TAGs	Triacylglycerols
SFC	Solid fat content
AMF	Anhydrous milk fat
SFAs	Saturated fatty acids
UFAs	Unsaturated fatty acids
MUFAs	Monounsaturated fatty acids
CMP	Caseinomacropeptide
PUFAs	Polyunsaturated fatty acids
MFGM	Milk fat globule membrane
ADV	Acid degree value
LCFA	Long-chain fatty acids
MCFA	Medium-chain fatty acids
SCFA	Short-chain fatty acids
FFAs	Free fatty acids
FAAs	Free amino acids
Arg	Arginine
Pro	Proline
Ser	Serine
Asn	Asparagine
DMS	Dimethyl sulfide
DMDS	Dimethyl disulfide
DMTS	Dimethyl trisulfide
HOSO	High-oleic sunflower oil
PCA	Plant-based cheese alternative

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