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Transglutaminase enzyme in dairy technology: A comprehensive review of functional roles and applications

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Abstract

Transglutaminases (EC 2.3.2.13) are enzymes that catalyze acyl transfer reactions, with the γ -carboxamide group of the glutamine residue in a peptide-bound protein being a donor. The main acceptor is the ϵ -amino group of lysine leading to the formation of ϵ -(γ -glutamyl) lysine iso-peptide crosslinks or deamidation products. Microbial transglutaminase (mTG), most of which is obtained from *Streptomyces mobaraensis*, has become a vital biocatalyst in the processing of dairy products due to its wide substrate specificity, calcium-independent activation, and good biochemical stability.

In milk, the mTG enzymes are used to form covalent bonds crosslinking the casein micelles. After heating the proteins under controlled conditions, the enzyme reactivity can also be extended to the protein fraction of whey, thus enabling the reinforced protein networks development that greatly controls gelation kinetics, viscoelastic behavior, water-holding property, and microstructural morphology of fermented milks, cheese, ice cream, and high protein drinks. Such enzymatic modifications provide the possibility of texture mapping, reduction of syneresis, increase of yields, and partial replacement of fat or synthetic stabilizers thereby offering greater formulation and processing freedom to the food producers. However, if the crosslinking is uncontrolled or the enzyme is used in excess, the sensory characteristics, the flow of the product, and the heat stability may be adversely impacted. Moreover, the incorporation of the enzyme into complex ingredient matrices leads to further difficulties such as dosage accuracy, reaction conditions optimization, and non-ideal interactions with polysaccharides, mineral salts, and proteins fractions that are in competition. Labeling transparency, the issue of immunogenicity of new epitopes, and the continuous consumer resistance to enzymatic protein modification technologies (Popularly known as "meat glue") still remain the two biggest hurdles in the regulatory framework and market acceptance of these products.

Keywords: Transglutaminase, *Streptomyces mobaraensis*, dairy protein engineering, texture modification, enzymatic processing, meat glue

Introduction

Protein engineering in modern dairy technology

The role of protein engineering in modern dairy production is constantly being redefined as a tool that opens up new ways of improving functional properties and therefore moves beyond those that can be achieved with thermal treatments, mechanical interventions, and fermentation methods alone (Romeih and Walker, 2017) ^[18]. By means of site-specific covalent and non-covalent alterations it is possible to gain full control over the ability of casein and whey proteins to dissolve, emulsify, gel, and hydrate (Bönisch *et al.*, 2007) ^[12]. Enzymatic treatments especially the ones that rely on the ability transglutaminase to bring about protein cross-linking have gained the greatest popularity among the methods of protein modification on account of their specificity, low impact on product quality, and the mild condition of their operation when compared to the chemical and physical methods (Moon *et al.*, 2009) ^[2]. Food-grade transglutaminases are special enzymes since they can catalyze covalent rearrangements of polypeptide chains that do not involve the change of amino acid composition and therefore, they allow the creation of fine microstructures while the nutritional value is retained (Yasmin *et al.*, 2021) ^[21].

Historical development and industrial adoption of transglutaminase

Scientists initially only found transglutaminase activity in animal tissues such as plasma coagulation Factor XIII and tissue transglutaminase, where the enzyme plays a role in blood clotting and helps stabilize the extracellular matrix (Gerrard, 2002)^[7]. However, later on it was discovered that microbial transglutaminases are considerably better for industrial purposes in that they can be produced cheaply, they have a wider range of substrates on which they can act, and they do not require calcium cofactors. As such, the use of transglutaminase has been greatly expanded since it was previously only a niche biochemical reagent and now it's a standard processing aid (Fatima and Khare, 2018)^[5]. When it comes to making dairy products, microbial transglutaminase (mTG) is especially suitable for casein-based systems, operating most efficiently at 35-50 °C and close to neutral pH, thus facilitating the integrating of mTG into milk, yoghurt, cheese, and protein drink lines that require only minimal installation of new equipment (Walstra *et al.*, 2006)^[19].

Microbial transglutaminase treatment of casein and whey proteins resulting in covalent crosslinking has been extensively studied and understood at molecular levels by recent papers using various experimental techniques such as SDS-PAGE and LC-MS/MS, light scattering, fluorescence and confocal microscopy, and rheological modeling in real dairy products. Although there are articles reviewing transglutaminase use in food generally, thorough discussions on dairy-specific applications that establish the molecular mechanism of crosslinking leading to changes in the microstructure of the gel, production parameters, regulations, and clean-label initiatives are very rare. The present review addresses this major void by covering enzymatic mechanisms, protein-structure-function relationships in milk proteins, differences in products, methods of process optimization, regulatory aspects, and possible future work for dairy technologists and biochemists in the field.

Transglutaminase: Enzymatic classification and biological sources

Comparative biochemistry of animal, plant and microbial transglutaminases

Transglutaminases constitute a phylogenetically diverse group of thiol-dependent acyltransferases which are widespread in nature in animals, plants, and microorganisms and are involved in a variety of cellular processes ranging from blood coagulation in vertebrates to fungal cell wall assembly and bacterial stress response (Serafini-Fracassini & Del Duca, 2008; Mamun & Maruyama, 2023)^[25, 24]. For example, mammalian tissue transglutaminases, like plasma Factor XIII and other isoforms, are calcium-dependent enzymes and their activation involves a series of conformational changes which results in quaternary complexes with highly regulated functions restricting their usage as food-grade biocatalysts despite their well-characterized biochemistry (Fox & McSweeney, 2017)^[6]. However, microbial transglutaminases differ in that they are single-polypeptide chains lacking calcium requirement and can be produced economically in large quantities via single-step submerged fermentation, and also their substrate range is very wide which has favored them for commercialization. Plant transglutaminases carry out essentially the same type

of transamidation reaction with peptide-bound glutamine but their large-scale extraction, standardization, and quality control present difficulties that have limited their use mainly to research laboratories and a few specialty applications (Prakasan *et al.*, 2015; Abou-Soliman *et al.*, 2020; Mamun & Maruyama, 2023)^[26, 27, 24].

Microbial transglutaminase from *Streptomyces mobaraensis*: Production and characterization

Microbial transglutaminase (mTG) that is commercially available is mostly derived from *Streptomyces mobaraensis* (a Gram-positive actinomycete that has also been named *Streptoverticillium mobaraense*). This organism has properties that make it a good candidate for submerged fermentation controlled by environmental factors and scalable purification. Also, the enzyme is secreted outside the cells directly into the medium which makes recovering it much easier and cheaper compared to the intracellular ones. Through several rounds of strain development, targeted genetic modifications and even genetic engineering, the resulting high-yield, high-stability, and high-purity strains capable of producing the desired microbes or antibiotics free are compatible with regulatory requirements (USDA-FDA, 2022).

Physicochemical and kinetic characteristics

The enzyme produced from *S. mobaraensis* is a single monomeric protein with a molecular weight of approximately 38 kDa. It is classified as EC 2.3.2.13 and the catalytic triad of cysteine, histidine, and aspartate that is used to form thioacyl intermediates. The enzyme has its highest-rate activity around a pH range of 5.0 to 8.0 and the enzyme is usually used close to pH 6.0-7.0 in dairy processing which naturally aligns with milk systems and not disrupt casein micelles before fermentation or renneting (Moon *et al.*, 2009)^[2].

Its temperature optima are 35 to 50 °C, but the enzyme activity still continues at a lower temperature if you incubate longer making it suitable for cold-processing dairy applications (Walstra *et al.*, 2006)^[19].

Commercial lyophilized forms provide a specific activity that may vary from hundreds to thousands of units per gram which is usually dosed at 1-20 U g⁻¹ protein in the dairy system for 30 min to even several hours depending on the level of crosslinking that is required (Gómez *et al.*, 2020)^[1]. Thanks to the specificity of its glutamine and lysine which are the only two residues that can be crosslinked, we can now talk about the site-specific modification of milk proteins by an enzyme without much off-target effect (Rosseto *et al.*, 2023)^[20].

Molecular mechanisms of transglutaminase action in dairy matrices

Enzymatic catalysis and ε-(γ-Glutamyl) lysine crosslink formation

Transglutaminase is an enzyme that catalyzes the acyl-transfer reaction which is reversible. Here, glutamine residues present in the peptides act as the acyl donor and the γ-carboxamide groups are involved. Next, the cysteine thiol within the enzyme's active site makes a nucleophilic attack to generate a thioacyl-enzyme intermediate which is very short-lived. Thioacyl intermediate is then transferred the acyl group to the next closest nucleophile. In the case of the dairy proteins, it is lysine's ε-amino group that acts as the

main acceptor. In the same chain (intramolecular) lysine or in (intermolecular) adjacent the chain Lys residue, the ϵ -(γ -glutamyl) lysine isopeptide bond is formed. This covalent bond is very stable due to its resistance both to denaturation and proteolysis. Without any primary amine available, the acyl group is transferred to water resulting glutamine deamidation to glutamic acid which changes the charge and hydrogen bonding in the local environment (Reitmaier *et al.*, 2025) ^[22].

These crosslinks convert the milk protein networks from non-covalent structures mainly supported by hydrophobic interactions, electrostatic forces, and mineral bridges to strong covalent hybrids with covalent junctions. As a result, the gel network's elasticity is enhanced, the stress at yield increases, and the gel is more resistant to heat or osmotic stress (García-Gómez *et al.*, 2019) ^[10].

They are, in normal processing, highly stable and resistant to hydrolysis, thus these bonds help create a structural memory of the network that lasts even after the enzymes have been inactivated by pasteurization or UHT treatment (Salunke & Metzger, 2023) ^[16].

Substrate specificity and accessibility in dairy protein substrates

The specificity of microbial transglutaminase (mTG) is influenced by the residues adjacent to the glutamines and lysines that are reactive, as well as the exposure of these residues in either native or unfolded protein states (Bönisch *et al.*, 2007) ^[12].

Among milk proteins, β -Casein and κ -casein, due to their flexible solvated regions that are rich in glutamines, are more easily crosslinked (Moon *et al.*, 2009) ^[2]. Whereas the tightly folded α s1-casein and whey proteins such as β -lactoglobulin limit access due to steric hindrance so that heat-induced unfolding is required for the enzymes to have access (Fox & McSweeney, 2017) ^[6]. Heat treatment of β -lactoglobulin or α -lactalbumin, or the formation of disulfide bonds with κ -casein on micelles, not only reveals hidden sites but also leads to casein-whey hybrid networks (Romeih & Walker, 2017) ^[18].

Kinetic studies conducted in model systems show that at pH 8.0-8.5, mTG is capable of polymerizing over 70% of β -lactoglobulin into large aggregates, thus reflecting an opposite preference for whey over caseins and a realization that heat, time, and pH must be tailor-controlled (Vasić *et al.*, 2023) ^[9]. Therefore, enzyme dosing strategies must be merged with processing routes to precisely crosslink the desired proteins at the critical steps.

Protein network formation and structural consequences

microbial transglutaminase, in either milk or model systems, produces a covalent reinforcement between casein micelles and whey proteins resulting in an interconnected network which is subject to the degree of reaction, protein content, minerals, and competing solutes (Walstra *et al.*, 2006) ^[19]. By means of crosslinking within the micelle, the stability of the micelle against calcium removal, ethanol or high pressure is improved where the ionic bridges are substituted by covalent isopeptide bonds (Reitmaier *et al.*, 2025) ^[22]. In the processes of yoghurt fermentation and cheese renneting, gelation is accelerated by the preformed networks which also enhance strength, modify pore structure, and reduce syneresis (Bönisch *et al.*, 2007) ^[12].

Simultaneous crosslinking of the denatured whey proteins with caseins leads to increased aggregate size and network density which results in augmenting the viscosity, yield, and water holding capacity of the fermented or coagulated products (Moon *et al.*, 2009) ^[2]. Such changes result in a unique rheology - higher storage modulus (G'), adjusted yield stress, and shear profiles - perfect for textural improvements as long as the processes do not lead to excessively stiff or grainy products (García-Gómez *et al.*, 2019) ^[10].

Transglutaminase interactions with dairy protein fractions

Casein micelle architecture, crosslinking, and colloidal stability

Casein micelles that are primarily composed of the subunits (α s1, α s2, β , and κ -casein) are complex colloidal particles where the subunits interact mainly through hydrophobic interactions and are also bridged by colloidal calcium phosphate (CCP) with the help of κ -casein forming a protective "hairy" layer on the surface that provides both steric and electrostatic stabilization to prevent aggregation (Walstra *et al.*, 2006) ^[19]. Microbial transglutaminase (mTG) action results in the formation of an extensive network of intramicellar crosslinks, especially between β - and κ -caseins, as shown by sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) analysis where the intensity of each protein band decreases and the high-molecular-weight polymers appear (Reitmaier *et al.*, 2025) ^[22]. The covalently strengthened micelles exhibit increased resistance to structural damage caused by CCP removal through chelators, ethanol addition, or high hydrostatic pressure (Moon *et al.*, 2009) ^[2].

At the molecular level, crosslinking may impede κ -casein mobility on the micelle surface, thus displacing steric and electrostatic protection and hence influencing renneting time, acid gelation rates, and interactions with heat-denatured whey proteins (Bönisch *et al.*, 2007) ^[12]. Since the improved mechanical properties and altered surface features are two competing effects that define the outcome, a moderate balance between these can be achieved by adjusting enzyme concentration (1-10 U g⁻¹ protein), temperature (30-40 °C), and incubation time (1-24 h) so as to fulfill the requirements of various products like UHT milk, yoghurt bases, or cheese milk (Fox & McSweeney, 2017) ^[7].

Whey protein biochemistry and enzymatic reactivity

Among all the milk proteins, particularly β -lactoglobulin (~36 kDa) as a major component of whey, exhibits relatively poor reactivity to microbial transglutaminase (mTG) in native milk systems. The main factor that determines this behavior is protein conformation. Most of the glutamine and lysine amino acids which are needed for enzymatic crosslinking are hidden inside the tightly folded tertiary structure of β -lactoglobulin hence, the enzyme cannot reach them easily (Romeih & Walker, 2017) ^[18]. The situation is drastically changed by heat treatment. Partial denaturation results in the disruption of the original folding in which the reactive residues are hidden. This also makes it possible for whey proteins to react with κ -casein at the surface of casein micelles via disulfide bonds. Thus, whey proteins become attached to the micellar matrix physically, which increases the likelihood of covalent bonding mediated

by mTG and stable casein-whey conjugates formation (Vasić *et al.*, 2023) ^[9].

Experimental data obtained using model systems illustrate that whey proteins can be extensively involved in enzymatic crosslinking if the conditions for the treatment are rigorously controlled. At mildly alkaline pH, mTG was able to convert over 70% of β -lactoglobulin into soluble and insoluble aggregates, thereby emphasizing the idea that this protein rather actively participates in network formation than simply filling the matrix (Gómez *et al.*, 2020) ^[1]. Such reactivity gives rise to a very high potential for the functional improvement of the final product such as enhanced viscosity, gel firmness, and thermal stability, especially in protein drinks and acid-induced gel-type products. Hence, efforts have been made to find the optimum preheating and pH adjustment combination before enzymatic treatment in order to get the greatest functional effect (Rosseto *et al.*, 2023) ^[20].

Still, the possibility of whey protein crosslinking being effective is only in a relatively limited time frame. Overzealous polymerization would be detrimental to solubility, the tendency to sediment through the sediment layer formation, and the development of off-textures like grittiness or chalkiness. Hence, these factors reveal that a balance between protein denaturation and enzymatic reaction kinetics is necessary so that one can achieve the desired level of structural reinforcement without compromising the sensory character of the product (García-Gómez *et al.*, 2019) ^[10].

Casein-whey hybrid protein networks and microstructural organization

mTG would facilitate covalent crosslinking of denatured whey proteins and casein micelles, creating hybrid protein networks in which soluble whey proteins are the molecular bridges connecting different micelles. Instead of forming separate aggregates, whey proteins get embedded in the continuous matrix thus, covalent crosslinking plays a role in the strengthening of the casein network (Bönisch *et al.*, 2007) ^[12]. Due to the mixture of different molecular species, the resulting hybrid network provides better performance in the textural quality of fermented dairy products such as yoghurt, fresh cheeses, and high-protein cultured beverages when compared to gels stabilized only by non-covalent interactions. The firmness of the gel, the amount of syneresis, and the mouthfeel all point to such advantages (Moon *et al.*, 2009) ^[2].

Microscopic features perfectly correspond to the changes observed at the macrolevel. Gels from dairy protein subjected to mTG had a smaller and more homogeneous pore size, the protein strands were more compact, and water-holding capacity was increased. These structural properties lead to enhanced smoothness and physical stability of the product, assuming protein crosslinking is not excessive (Reitmaier *et al.*, 2025) ^[22]. It should be emphasized that such protein networks are only one phase in a multiphase system; therefore, interaction with fat globules, hydrocolloids, and mineral ions also plays a role in determining the final product structure. There is no doubt that this fact further strengthens the argument that formulation with mTG should be part of an overall processing strategy and is not a treatment by itself.

From the nutrition aspect, formation of crosslinked ϵ -(γ -glutamyl) lysine may slightly alter the protein digestion

profile and the release of bioactive peptides due to changes in hydrolysis patterns. In a certain way, these modifications impact amino acid availability and satiety responses, even if their physiological significance still requires further investigations.

Product-specific applications in dairy processing

In the dairy industry, microbial transglutaminase (mTG) is increasingly used as a processing aid as it offers a great degree of control over the protein crosslinking phenomenon to suit the different requirements of the final products. This power of the enzyme is taken advantage of by the industry to manufacture a large variety of dairy products with improved texture, increased stability, and higher yields by simply tweaking the enzyme dosage (generally 1-20 U g⁻¹ protein), temperature of incubation (30-50 °C), pH (6.0-7.0), and reaction time (30 minutes-24 hours). Protein crosslinking is most efficient when treatments are performed on protein substrates that are readily available such as before heat processing, fermentation, or renneting (Romeih & Walker, 2017) ^[18].

This enzyme silica allows for reinforcement of casein micelles as well as whey protein aggregates thereby enhancing the strength and elastic properties of resulting gels. Better water retention and textural stability are often associated with higher product yields and longer shelf life where one difficulty in dairy production, such as moisture loss, is addressed (Rosseto *et al.*, 2023) ^[20]. Moreover, the treatment has limited detrimental effects on the nutritional value of milk proteins.

Ultra-high-temperature and recombined milk formulations:

mTG has essentially been shown to stabilize fluid milk, especially UHT and recombined milk, which are typical of gel formation and sedimentation on storage. Crosslinking of proteins inside casein micelles reinforces molecules thus, mTG-treated casein where the calcium phosphate is partially dissolved, is more resistant to disruption in the particle structure by heat treatment that is more extreme (Walstra *et al.*, 2006) ^[19]. A typical dosage for mTG would be 2-5 U g⁻¹ protein, and the enzyme would be allowed to work at 40 °C for 1-2 h. Turning the milk into cream by homogenization and then sterilizing it by ultra-high temperature treatment (135-150 °C for 4-10 s) follow this treatment. Improvements in shelf life that are visible enough to take advantage of 6-12 month storage at room temperature have been reported under these conditions, along with smaller viscosity increases and less aggregation. Similar advantages are provided by recombined milks that are made up of concentrated proteins. Casein micelles which are crosslinked become rehydrated better, become more soluble, and their resistance to phase separation is elevated. All three features are greatly desired in the distribution chain where the product is exposed to higher temperatures for longer durations (Moon *et al.*, 2009) ^[2]. All in all, these effects contribute to the maintenance of sensory quality and also increase the solids content of the product without causing excessive thickening. Thus, the processor has more freedom when it comes to product design (Romeih & Walker, 2017) ^[18].

Yoghurt and fermented milk formulations

Among the many commercial dairy applications of microbial transglutaminase, yoghurt production is

undoubtedly the oldest and most successful one. The influence of mTG can be mainly noticed in the increase of the gel strength of acidified proteins when it is used in the pretreatment, concurrent with the starter culture addition (typically 1-10 U g⁻¹ protein at 37-45 °C for 1-4 h), resurfacing a higher density and stability of protein junctions (Bönisch *et al.*, 2007) ^[12]. It works overall to harden the texture with the storage moduli (G') appreciation of around 20-50% and alongside a major decrease in syneresis (30-70%) and increased water-holding capacity. Concerning these changes, it turned out that they were more beneficial for low-fat yoghurts that due to the weakened protein network suffer in texture as well as stability (García-Gómez *et al.*, 2019) ^[10].

The time at which the processing takes place is very important in this context. Whereas pre-fermentation enzyme treatment results in a finer, more homogeneous microstructure, it is crucial for simultaneous enzyme and starter addition to be adjusted kinetically so as not to lead to a decrease in culture viability during the extension of incubation time at about 42 °C (Gómez *et al.*, 2020) ^[1]. The findings of the long-term storage studies are consistent with observed mTG durability in that gel strength and whey separation indices were preserved in mTG-treated yoghurt after 56 days of storage at 4-6 °C, whereas control samples underwent degradation (Rosseto *et al.*, 2023) ^[20].

Cheese production and processed cheese formulations

mTG is a functional ingredient that is frequently used to not only increase the yield of cheese curd but also to improve the textural properties of the final cheese by means of casein crosslinking. As regards production, the enzyme is typically added at levels of 5 to 15 units per protein gram about 20 to 30 minutes after rennet and the mixture is then incubated for 30 to 60 minutes at the temperature range of 30 to 35 °C in order to achieve an increase of 5 to 15% in yield (Moon *et al.*, 2009) ^[2].

Fresh and semi-soft cheeses prepared by this approach show higher moisture content accompanied by improved softness and enhanced sliceability characteristics, which can be attributed to more open, serum-retaining protein matrices that allow a faster rate of enzymatic breakdown during ripening. One observation worth noting is that proteolysis is still largely unaffected. During a ripening period of 90 days, for example, a water-soluble nitrogen increment of only 5% (slight) has been recorded by mTG-treated cheeses, meaning that enzyme accessibility and flavor development were maintained (Salunke & Metzger, 2023) ^[16]. These kinds of changes at higher enzyme concentrations (10-20 U g⁻¹ protein) reinforce the melt structure thereby reducing oiling-off, as well as lowering the dependence on phosphate emulsifying salts in processed cheese systems. The spreadability of these products remains constant during melt at high temperatures (80-90 °C) and storage as well (Prakasan *et al.*, 2015; Fatima & Khare, 2018) ^[26, 5].

Ice cream and frozen dessert formulations

One major success of mTG utilization is the ability of the enzyme to yield stabilized gel structures that may even be thermodynamically unfavored. With a view to formulating healthy products, ice cream can be made to a large extent without fat, but its texture and functional properties usually worsen notably. Proper application of mTG has been shown to result in improved texture and functionality even in

reduced-fat ice cream. A good level of enzyme for this purpose would be 2-8 U g⁻¹ protein, with the treatment taking place at 35-45 °C for 1-2 h before freezing, as performing this treatment helps to reinforce the serum protein network and to significantly improve four-dimensional features such as shape retention, melt resistance, and perceived creaminess. Via a combination of effects, mTG crosslinking also achieves other desirable attributes of low-fat ice cream such as a 20-40% increase in viscosity, partial promotion of fat coalescence, and restriction of ice crystal growth during freeze-thaw cycling. Having said that, the products were still perceived to be the equivalent of full-fat ones (Romeih & Walker, 2017) ^[18]. Addition of inulin or certain hydrocolloids would further promote mTG water binding thereby resulting in 20-50-minute extension of meltdown time at 20 °C (Gómez *et al.*, 2020) ^[1]. Sensory panels unanimously voted for these products since they were less cold and smoother, thus giving credibility to the role of enzyme in clean-label strategies for fat reduction without sacrificing consumer acceptance (Rosseto *et al.*, 2023) ^[20].

Milk protein ingredients and ready-to-drink beverages

In terms of finished product utilization, the milk protein ingredients after being treated with microbial transglutaminase (mTG) such as micellar casein and milk protein concentrates (MPC) have been ramped up in both ready-to-drink (RTD) and high-protein beverage applications. Generally, running the moderate process (5-20 U g⁻¹ protein, pH 7.0, 40 °C for 2-4 h) results in enhanced protein solubility, emulsifying capacity, and markedly controlled gelation behavior. When crosslinked MPC is incorporated into RTD shakes that contain a protein concentration in the range from 8 to 12%, fouling due to UHT and sedimentation is significantly reduced all the while physical stability is maintained for a six-month period of ambient temperature (20 °C) storage (Vasić *et al.*, 2023) ^[9].

Similarly, the impact of mTG into sodium caseinate has been demonstrated through thermal transition temperature increments by around 5-10 °C enhancing melt control in cheese-related applications (Gerrard *et al.*, 2002) ^[7]. These combined functional properties of MCCI and MPC to respond to mTG are able to cut back the hydrocolloid content regularly used in forming fat-reduced RTD beverages with stable viscosity and mouthfeel, while at the same time their sensory profile resembles that of full-fat (Romeih & Walker, 2017) ^[18].

Technological advantages and process benefits

Enzymatic protein crosslinking using transglutaminase (TGase) offers many technological benefits that are directly in line with the key goals of the industry such as increased process efficiency, lowered formulation costs, and improved sensory and functional qualities of dairy products (Fox & McSweeney, 2017) ^[6].

Precision texture engineering

Covalent protein cross-linking can be used to tailor textural properties to an even greater extent than gel firmness, cohesiveness, and shear-thinning behavior. For example, in yogurt mixtures, this is demonstrated by a 20-50% increase in storage modulus (G'), whereas in cheese production, the development of hardness during ripening becomes more

predictable. Such benefits are not only achieved with less hydrocolloid stabilizers but also without the generation of off-flavors or compromising sensory acceptance (Bönisch *et al.*, 2007) ^[12].

Improved water-holding capacity

Crosslinked protein networks have a much stronger ability to bind serum and thus result in significant decreases of syneresis, for instance, by 30-70% in yoghurts, and higher cheese yields due to the formation of finer and more uniform microstructures. In frozen dairy desserts, the immobilization of free water within dense protein gels increases resistance to meltdown and structural collapse (Reitmaier *et al.*, 2025) ^[22].

Support for fat and soluble carbohydrate reduction

Microbial transglutaminase (mTG) helps to produce lean or reformulated products by strengthening protein interactions in low-fat yoghurts, ice creams, and reduced-sugar beverages. As a result, creaminess, viscosity, and stability are preserved even though the fat or emulsifier content is reduced by 20-50% (Moon *et al.*, 2009) ^[2].

Process consistency and batch uniformity

Protein systems stabilized by enzymes are less susceptible to changes in the composition of raw milk, thus contributing to the durability of thermal stability in UHT milk and more accurately proteolysis during cheese ripening. Consequently, these changes prolong shelf life because the buildup of viscosity and the phase separation slow down during storage (Walstra *et al.*, 2006) ^[19].

Limitations, challenges, and mitigation strategies

Transglutaminase (TGase) is broadly applicable, but the enzyme in dairy processing leads to several biophysical and operational issues that, if not handled properly, can have a negative impact on product quality (Romeih & Walker, 2017) ^[18].

Over-crosslinking and textural defects

Too much enzyme or exposure for too long (generally above 20 U g⁻¹ protein) causes protein networks to become too dense. As a result, textural properties become undesirable due to extreme firmness, gritty texture, or rubber-like sensation in yoghurts and cheeses (Bönisch *et al.*, 2007) ^[12]. Also, over crosslinking in UHT milk speeds up age-thickening since protein mobility is limited, with viscosity sometimes going beyond 100 mPa·s after 3-6 months of storage at 20 °C (Moon *et al.*, 2009) ^[2].

Besides that, the ε-(γ-glutamyl) lysine bonds that are formed are not broken down by proteolysis and therefore normal flavor development and texture evolution during cheese ripening (6-12 months) gets disrupted (Reitmaier *et al.*, 2025) ^[22]. Measures to lessen the above effects involve short incubation times (about 2 hr at 40 °C), fast thermal inactivation (72 °C for 15 s), and accurate enzyme dosing so that controlled crosslink density is maintained (García-Gómez *et al.*, 2018) ^[11].

Processing and operational constraints

Transglutaminase has a narrow pH range (6.5-7.5) and temperature range (35-50 °C) where it works best, so it is not very effective in acidic fermentations (pH < 5.0) or in cold-processed systems. At pH values above 8.0 or

temperatures below 25 °C, the enzyme activity may decrease by 50-80% (Fatima & Khare, 2018) ^[15]. Although whey protein pre-denaturation can expose enzyme sites, it also makes the protein more likely to aggregate when high solids are present. At the industrial level, the uneven distribution of enzymes in big processing tanks can cause the gel strength to vary by as much as 30%. Besides, enzyme costs, which are typically 0.5-2 €/kg of product, can be a major obstacle to the economic feasibility of high-volume dairy applications unless increased yields or better quality can offset the costs.

Ingredient interactions and functional synergies

The activity of transglutaminase is also regulated by the interactions it has with other parts of the product. With high salt concentrations (> 0.1 M NaCl) or presence of divalent cations, enzyme activity can be reduced by 20-50% due to electrostatic shielding, thus making it difficult to apply the enzyme in brined cheeses and mineral-fortified beverages (Romeih & Walker, 2017) ^[18]. Polysaccharides such as pectin or guar gum may sterically hinder enzyme access to protein substrates, and as a result, crosslinking efficiency in yoghurt systems is reduced by 15-25%. Similar decreases have been noted in ice cream formulations owing to the presence of fat globules and phenolic compounds (Gómez *et al.*, 2020; Rosseto *et al.*, 2023) ^[1, 20]. Sequential processing methods, such as adding the enzyme before stabilizers or fats, have been shown to be successful in reducing these interactions, but they require careful process redesign (Prakasan *et al.*, 2015) ^[26].

Safety assessment, regulatory framework, and clean-label positioning

Toxicological safety and digestive fate

Food Chemicals Codex and JECFA-compliant transglutaminase preparations have proven a very safe bioprofile on toxicological tests. No signs of acute toxicity, genotoxicity, or subchronic adverse effects were found at levels of 1000 mg/kg body weight per day in rodents. Although ε-(γ-glutamyl) lysine isopeptide bonds resist gastric pepsin, they are efficiently cut by intestinal peptidases and renal aminopeptidases, thus lysine bioavailability is maintained along with overall protein nutritional quality. The peptide profiles upon *in vitro* digestion are similar to those of native casein. Furthermore, cross-linking of whey-soy mixtures has been found to hide certain allergenic epitopes, thereby potentially lowering allergenicity. While there have been a few cases of occupational sensitization and theoretical concerns about gluten mimicry, these issues have led to continued monitoring. So far, epidemiological evidence has not indicated that consumption of dairy products treated with transglutaminase is associated with any health problems.

Regulatory status across jurisdictions

The U.S. FDA has given GRAS to certain microbial transglutaminase (mTG) preparations (*e.g.*, GRN 1021 and GRN, 1139) for use in dairy industries up to 100 mg total organic solids per kilogram of product, requiring allergen labeling when milk-derived carriers are used. EFSA considers transglutaminase from *Streptomyces mobaraensis* as a safe processing aid in accordance with Regulation (EC) No 1332/2008 and has not identified any residual safety concerns following thermal inactivation. On the other hand,

the FSSAI in India allows the use of transglutaminase only in selected dairy categories under the Food Safety and Standards Regulations (2010), consistent with Codex STAN 192-1995, but it disallows undisclosed use of transglutaminase as a protein binder in traditional dairy products like paneer and curd. These differences in regulation reflect India's somewhat cautious approach to the use of processing aids in traditional dairy products.

Consumer perception and clean-label considerations

Consumer perception of transglutaminase is still divided, with the enzyme frequently being linked with "meat gluing" and ultraprocessing. Survey results indicate that 40-60% of people will not accept these enzymes if they are not clearly informed about the functionalities, *e.g.*, better texture of low-fat products. Therefore, clean-label movement embraces openly disclosing ingredients through voluntary (*e.g.*, "enzymatically treated") and digital forms such as QR codes that link to safety tests and regulatory permissions (Romeih & Walker, 2017) ^[18]. While proposed hypoallergenic benefits of crosslinking technology seem promising especially in infant formula and specialty beverage applications, they still require strong support before going public. Overall, transparent labeling together with consumer education is fundamental to gaining trust especially in the Asia-Pacific markets where regulation intensification is evident (FSSAI, 2022).

Emerging innovations and recent technological advances

New investigations have movingly targeted the elimination of long-standing problems with the TGase (transglutaminase) that have mainly been over-crosslinking, high enzyme costs, and limited compatibility with complex food matrices. These will be basically achieved through nanotechnologies, bioengineering, and process engineering that integrates biological functions, structures, and systems to create new or modified products, more efficiently and sustainably.

Enzyme immobilization and recycling technologies

Immobilization of mTG has been proven to be an excellent approach to enhance the economic and operational performance. mTG that chemically attached to magnetic nanoparticles (MNPs), cross-linked enzyme aggregates (CLEAs), or temperature-responsive polymers like poly (N-isopropylacrylamide) (PNIPAAm) has been revealed (infected with a virus) to keep, and in some cases even slightly, increase the catalytic activity (90-110% of the native enzyme). Normally, these two at least can withstand 5-10 reuse cycles and show marked improvements in thermal stability that allow the enzymes to be kept vivo and be active at temperatures up to 50 °C.

In mTG/ MNP based protein crosslinking systems for yogurt gel manufacturing could therefore rely on simple magnetic separation to recover the enzyme and reuse it in subsequent operations. Up to 70% savings in enzyme-related costs can be realized, according to a report on semi-continuous processing using magnetic separation (Gharibzahedi *et al.*, 2018). Altogether, enzyme stabilization and recycling technologies are likely to scale up to the industry-level easily and at the same time be environmentally friendly since less enzyme waste is generated.

Multi-enzyme combination strategies

An enzyme synergy system is a concept that has attracted considerable interest among researchers because it provides an opportunity of controlling the degree of protein modification beyond that achieved by mTG alone. For instance, the combination of mTG sequentially crosslinking followed by restrained protease hydrolysis (*i.e.*, Alcalase) of milk protein concentrate has been reported to give about a 30% increment in protein solubility and also accomplishing a reduction in bitterness in ready-to-drink beverages (Fatima & Khare, 2018) ^[5]. Even more sophisticated hybrid systems involving mTG and oxidative enzymes such as laccase or tyrosinase have been shown to create two types of protein networks via isopeptide and di-tyrosine bonds. The resulting robust structures are able to provide better colloidal stability and hence, prolong the shelf life of dairy products fortified with milk proteins. This is a good indication that multi-enzyme technologies may be employed in advanced dairy formulations in the near future (Gerrard *et al.*, 2002) ^[7].

Precision dosing and kinetics modelling

The latest development in instrumentation and software enables more accurate mTG applications. LC-MS/MS analysis coupled with molecular dynamics simulations helped to reveal glutamine-lysine reaction hotspots in milk proteins thus contributing to reducing enzyme dosage to less than 5 U g⁻¹ of protein, hence, the least danger of protein over-crosslinking (Lorenzoni *et al.*, 2022). Other innovations in the bioprocessing area involve pulsed enzyme dosing which is effective in limiting excessive crosslink formation in UHT milk while retaining the desired functional properties (Reitmaier *et al.*, 2025) ^[22].

Hybrid dairy formulation systems

A series of mTG and different non-thermal processing technologies such as high-pressure processing (400-600 MPa) and ultrasound have been used to enable enzymatic cross-linking under cold conditions preserving heat-sensitive biocomponents like probiotics in yoghurts (Rosseto *et al.*, 2023) ^[20]. Similarly, immunoglobulin E (IgE) binding to casein in casein-soy blends or plant-casein mixtures can be lowered by approximately 50% via epitope masking through the mTG treatment. Such results offer potential strategies for producing hypo-allergenic dairy-based beverages that will be most fitting for susceptible consumer groups (Sharma *et al.*, 2023).

Patent landscape and innovation trends

Patent filings related to immobilized mTG systems, and plant-dairy hybrid formulation, were about 25% more in 2025 than the previous five years, signifying that industries are becoming more interested in these technologies (European Patent Office, 2024). Current technology trends are focused on features like bioengineered production strains with CRISPR-edited *Streptomyces* species capable of up to two-fold yield improvements and dual-enzyme systems with dienzymes that support clean-label fibre enrichment. Despite this progress, notable gaps remain, particularly in Asia-Pacific techno-economic assessments and integrated intellectual property strategies linking food manufacturing with medical and biomaterial applications, including TGase-crosslinked casein wound dressings (Gharibzahedi *et al.*, 2018).

Future research priorities and knowledge gaps

The incorporation of novel technologies and changing market demand gradually promote transglutaminase from a conventional flavoring enzyme to a central tool in precision dairy engineering. This shift provides a good window of opportunity to apply computational modelling, advanced delivery systems, and omics-driven research in order to fill existing knowledge gaps (Fox & McSweeney, 2017) ^[6].

Precision enzyme dosing and real-time process monitoring

Combining real-time Raman and near-infrared spectroscopic methods with machine learning models is an innovative way of estimating crosslinking kinetics of mTG against intrinsic milk variables such as casein to whey protein ratio, mineral composition, and pH variation. If implemented, these systems may permit dynamic enzyme dosing within the power of 0.5 to 15 U g⁻¹ protein, so that desired crosslink densities are obtained having less than 10% variability. Nevertheless, there still are significant hurdles to the adoption of inline sensor technologies by large-scale dairy plants. One of the biggest issues is how to get robust validation through LC-MS/MS quantification of ϵ -(γ -glutamyl)lysine bonds when dealing with seasonal and geographical milk variations.

Smart, stimuli-responsive dairy matrices

Smart dairy matrices with immobilized mTG incorporated in temperature or pH-responsive hydrogels can be considered as a very attractive concept, yet it awaits more intensive research. They can be predictably designed in such a way that enzymatic crosslinking would be triggered (e.g., 40 °C and pH 6.5-7.0) in ultra-high-temperature processing lines or even in the 3-dimensional cheese manufacturing platforms of the future. In addition to that, proteins hybrids reinforced with antifreeze protein polypeptides (AFPs) or nanocellulose fibres could be potential candidates for the improvement of frozen dessert stability. However, interaction of mTG crosslinking with such molecular reinforcement mechanisms remains quite unexplored and requires not only *in vitro* but also *in vivo* investigations besides (Gerrard *et al.*, 2002) ^[7].

Nutritional applications and bioactive modulation

By targeting mTG in milk protein concentrate, usage levels can be controlled in order to affect proteolytic degradation kinetics of the gastrointestinal tract. This level of control opens the door to a wide range of nutritional benefits such as lowered glycemic response, increased satiety, and faster muscle protein synthesis for sports recovery. One of the major issues that still need to be worked out is the lack of controlled clinical human trials that directly assess the impact of crosslink densities on postprandial metabolic changes. Artificial intelligence (AI) in formulating protein blends for the elderly with dysphagia or for athletes' recovery is definitely a highly promising commercial route but must be supported with data on safety, efficacy, and regulatory compliance (Rosseto *et al.*, 2023) ^[20].

Bioeconomy integration and sustainability development

Asia-Pacific dairy manufacturing sector scale-up interventions should encompass comprehensive techno-economic studies coupled with the development of regional bioeconomy-aligned intellectual property strategies (Fatima

& Khare, 2018) ^[5]. Utilization of mTG in environmentally friendly packaging materials and wound-healing films based on casein is bridging the gap between traditional food processing and biomedicine as well as therapeutic technologies.

Conclusion

Milk proteins can be chemically crosslinked by transglutaminase (TGase) that plays an important role in modulating the structural and functional properties of dairy protein systems. Thus, it provides dairy manufacturers with a versatile platform for multiple functionalities including texture control, high yield, and clean-label. TGase can be used in fluid milk and the fermented products, cheese, frozen desserts, and functional protein ingredients (Romeih & Walker, 2017) ^[18]. It is the enzyme's unique biochemical mechanism, i.e., the formation of ϵ -(γ -glutamyl) lysine isopeptide bonds with the casein micelles' native structure and whey proteins' reactivity that allow those protein networks to be fortified and consequently, the improved rheological properties and enhanced colloidal stability under processing stress, such as heat, osmotic and mechanical stress, are the results (Bönisch *et al.*, 2007) ^[12].

Meanwhile, some challenges such as over-crosslinking, process control and complex interactions among ingredients remain. Thanks to continuous technological advances though, today's limitations keep on shrinking. Application precision was significantly enhanced as a result of improvements in enzyme immobilization, multi-enzyme use, as well as process monitoring and control, while operational flexibility also went up. In addition, safety of transglutaminase use in dairy processing is strongly supported by extensive toxicological studies and international regulatory approvals. Future industrial utilization will rest largely on the integration of deep mechanistic knowledge, economic viability and sound processing considerations. In that event, transglutaminase may well be the mainstay technology for sustainable and high performing dairy production systems of the future. Further research is focused on precise enzyme dosing regimens, stimuli-responsive dairy matrix systems, personalized nutrition and bioeconomy integration to name just a few. Overall, transglutaminase is positioned to be a platform technology with the transformative capability of next-generation dairy innovations and to respond to the continuous changes that consumer demand, regulatory frameworks and sustainability objectives bring about.

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