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Exploring Amylolytic Enzymes from GH Families in Maltooligosaccharide Biosynthesis: Classification, Catalysis, and Industrial Potential

Afifah Nurul Ilmi * and Enny Zulaika

Department of Biology, Faculty of Science and Data Analytics, Sepuluh Nopember Institute of Technology, Surabaya 60111, Indonesia.

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Abstract

Amylolytic enzymes, including α-amylase, β-amylase, and glucoamylase, are crucial in starch degradation and maltooligosaccharide (MOS) biosynthesis. Glycoside hydrolases (GHs), notably from families GH13, GH14, GH15, GH57, GH119, and GH126, offer high substrate specificity and catalytic efficiency under mild conditions. Their ability to produce MOS with prebiotic and functional properties underpins their growing relevance in food, pharmaceutical, and biofuel industries. This review highlights the classification, catalytic mechanisms, sources, and production techniques of these enzymes. It also discusses critical factors affecting enzyme activity—pH, temperature, substrate concentration, and metal ion activators—and explores their structural and biochemical characteristics for industrial applications. Finally, challenges such as enzyme stability and cost-efficiency are outlined alongside future prospects involving synthetic biology and process optimization for sustainable MOS production.

Keywords: Amylolytic enzyme; Glycoside hydrolases; Maltooligosaccharide; Biosynthesis

1. Introduction

Amylolytic enzymes are a group of hydrolases that catalyze the breakdown of starch and related polysaccharides into smaller oligosaccharides and simple sugars [1]. These enzymes, including α-amylase, β-amylase, and glucoamylase, play a pivotal role in carbohydrate metabolism and have been extensively applied in various industrial processes, particularly in food, fermentation, and biofuel industries [2]. Maltooligosaccharides (MOS) are the result of partial hydrolysis of amylose or starch, composed of linear chains of α-1,4-linked glucose residues have garnered increasing attention due to their versatile applications [3]. MOS exhibit several beneficial physicochemical and physiological properties, such as mild sweetness, low caloric content, high water retention, and prebiotic activity, these characteristics make MOS suitable for use as functional food ingredients, bulking agents, and stabilizers in pharmaceuticals and cosmetics [3,4]. Traditionally, MOS are produced through partial hydrolysis of starch, the demand for more efficient and selective production methods has shifted attention toward enzyme-based biosynthesis approaches, which offer high substrate specificity, environmentally benign conditions, and the ability to tailor product profiles [4,5]. Recent advances in enzymology and genomics have facilitated the discovery and characterization of novel glycoside hydrolases (GHs) involved in MOS biosynthesis. Enzymes from several GH families, particularly GH13, GH14, GH15, GH57, GH119, and GH126 have been identified as key catalysts in the degradation of starch and the synthesis of specific MOS products [6]. Understanding the classification, catalytic mechanisms, and structure-function relationships of these GHs is critical for optimizing enzyme performance and engineering tailor-made biocatalysts for industrial use [6,7]. This study aims to provide a comprehensive overview of the amylolytic GH families involved in MOS production, emphasizing their biochemical properties, reaction mechanisms, and industrial relevance. Through a detailed analysis

* Corresponding author: Afifah Nurul Ilmi

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of enzyme structure, function, and application, this work contributes to a deeper understanding of enzyme-based MOS biosynthesis and its implications for sustainable and value-added carbohydrate processing.

2. Classification of Amylolytic Enzymes

Amylolytic enzymes responsible for starch and maltodextrin hydrolysis are predominantly classified into several glycoside hydrolase (GH) families, including GH13, GH14, GH15, GH57, GH119, and GH126, based on sequence similarity and catalytic mechanisms, as can be seen in (Table 1), the specificities in the amylolytic enzymes GH families [8, 9]. Among these, GH13 is the largest and most diverse family, encompassing α-amylases, pullulanases, and maltogenic amylases, which act primarily via an endo-hydrolytic mechanism on α-1,4 and sometimes α-1,6 glycosidic bonds [10]. β-amylase (α-1,4-glucan maltohydrolase; EC 3.2.1.2; CAZy family GH14) is an inverting glycoside hydrolase that functions as an exo-hydrolase, facilitating the release of β-maltose units (via α-inversion) from the non-reducing ends of α-1,4-linked oligo- and polyglucans. This enzyme is likely essential as a biocatalyst in the degradation of starch, especially during the germination phase in plants, and is believed to play a significant role in overall plant metabolic processes [11]. GH15 includes glucoamylases and α-glucosidases that typically exhibit exo-acting behavior, hydrolyzing glucose units from the non-reducing ends of maltooligosaccharides. GH57 and GH119 contain thermostable and less-characterized α-amylases with unique structural folds adapted to extreme environments. Phylogenetic analyses based on conserved catalytic domains have enabled sequence-based classification and revealed evolutionary relationships among these families and subfamilies [12,13]. The GH126 amylolytic enzymes represent a newly established family of glycoside hydrolases, initially characterized by the protein CPF_2247 from *Clostridium perfringens*, which exhibits a potential α-amylase activity and adopts a distinct $(\alpha/\alpha)_6$-barrel catalytic fold. This structural configuration sets GH126 apart from other α-amylase families such as GH13, GH57, and GH119 [14].

Table 1 Specificities in the amylolytic enzymes GH families

Family	Enzyme	EC No.	Family	Enzyme	EC No.
GH 13	α-Amylase	3.2.1.1		Glucan debranching enzyme	2.4.1.25/3.2.1.33
	Oligo-1,6-glucosidase	3.2.1.10		Oligosaccharide α-4-glucosyltransferase	2.4.1.161
	α-Glucosidase	3.2.1.20		α-1,3-Glucan synthase	2.4.1.183
	Pullulanase	3.2.1.41		Isocyclomaltooligosaccharide glucanotransferase	2.4.1.248
	Amylopullulanase	3.2.1.1/41		Sucrose-6(F)-phosphate phosphorylase	2.4.1.329
	Sucrose α-glucosidase	3.2.1.48		Glucosylglycerate phosphorylase	2.4.1.352
	Cyclomaltodextrinase	3.2.1.54		Glucosylglycerol phosphorylase	2.4.1.359
	Maltotetraose-forming amylase	3.2.1.60		α-1,4-Glucan: phosphate α-maltosyltransferase	2.4.99.16
	Isoamylase	3.2.1.68		Isomaltulose synthase	5.4.99.11
	Dextran glucosidase	3.2.1.70		Maltooligosyltrehalose synthase	5.4.99.15
	Trehalose 6-phosphate hydrolase	3.2.1.93		Trehalose synthase	5.4.99.16
	Maltohexaose-forming amylase	3.2.1.98	GH 14	β-amylase	3.2.1.2
	Maltotriose-forming amylase	3.2.1.116	GH 15	Glucoamylase	3.2.1.3
	Maltogenic amylase	3.2.1.133	GH 57	α-Amylase	3.2.1.1

	Neopullulanase	3.2.1.135		Maltogenic amylase	3.2.1.133
	Maltooligosyltrehalose trehalohydrolase	3.2.1.141		Amylopullulanase	3.2.1.1/41
	Maltopentaose-forming amylase	3.2.1.-		Cyclomaltodextrinase	3.2.1.54
	Sucrose hydrolase	3.2.1.-		α-Galactosidase	3.2.1.22
	Cyclic α-maltosyl-1,6-maltose hydrolase	3.2.1.-		Non-specified amylase	3.2.1.-
	Amylosucrase	2.4.1.4		Glucan branching enzyme	2.4.1.18
	Sucrose phosphorylase	2.4.1.7		4-α-Glucanotransferase	2.4.1.25
	Glucan branching enzyme	2.4.1.18	GH 119	α-Amylase	3.2.1.1
	Cyclodextrin glucanotransferase	2.4.1.19	GH 126	α-Amylase	3.2.1.1
	4-α-Glucanotransferase	2.4.1.25			

3. Source of Enzymes

Enzymes can be derived from various biological sources, including animals (e.g., chymosin, pepsin, trypsin), plants (e.g., ficin, papain, bromelain), and microorganisms (e.g., pectinases, glucoamylase, α-amylase) [15]. The source of the enzyme significantly influences its availability, cost-effectiveness, ease of extraction, and other operational factors. Microorganisms, in particular, offer a versatile platform for enzyme production, as they are capable of synthesizing a broad spectrum of enzymes analogous to those found in animal and plant systems [15]. The industrial preference for microbial enzymes are preferred due to several advantageous features: microbial sources are abundant and easy to cultivate; the production process can be precisely controlled; commercial preparations are standardized; and the enzyme market benefits from competitive suppliers [16]. Moreover, microbial strains typically exhibit high growth rates, enabling the large-scale production of enzymes within a short timeframe. These strains are also amenable to genetic engineering—especially through recombinant DNA technology—which can enhance enzyme yield and specificity. Bacterial host strains that are commonly used are *Escherichia coli, Bacillus subtilis, Bacillus licheniformis,* and *Bacillus amyloliquefaciens*. Since many microbial strains are capable of producing multiple enzymes simultaneously, fermentation conditions can be optimized to favor the production of a target enzyme while suppressing others, allowing manufacturers to adapt to market demands [17,18]. However, in the context of food-grade enzymes, regulatory compliance necessitates full disclosure of whether the enzyme-producing microorganism has been genetically modified. This requirement stems from stringent legal frameworks which may classify such enzymes—and the foods produced using them—as "novel," thus subjecting them to additional safety assessments and approval processes [19].

4. Enzyme Production

Submerged fermentation (SmF) and solid-state fermentation (SSF) are two widely used microbial cultivation techniques, each with distinct characteristics and applications. Both fermentation types play crucial roles in biotechnology, with selection depending on the target product and microbial strain [20].

4.1. SmF (Submerged Fermentation)

Submerged fermentation (SmF) employs liquid substrates like molasses and nutrient broths. A major difference between submerged cultivation and solid-state cultivations is therefore the amount of free liquid in the substrate [21]. During the process, bioactive compounds are released into the fermentation medium. Since the substrates are consumed quickly, they must be regularly replenished with nutrients. This method is particularly suitable for microorganisms like bacteria that thrive in high-moisture environments. One of the key benefits of SmF is the relative ease of product purification. It is mainly applied for producing secondary metabolites intended for use in liquid form [22]. While submerged fermentation typically uses expensive media, costs may be reduced by incorporating solid-state fermentation using agricultural residues [23]. Unprocessed ingredients may need processing to extract and solubilize the nutrients with defined media good reproducibility is possible. A wide range of products can be produced, from a wide range of microorganisms and fungi. Many products are produced best under submerged cultivation [21].

4.2. SSF (Solid State Fermentation)

Solid-state fermentation (SSF) makes use of solid materials such as bran, bagasse, and paper pulp as substrates. A major benefit of this approach is the ability to recycle nutrient-rich waste products for fermentation. In SSF, substrate consumption occurs gradually over time, allowing for extended fermentation periods using the same material. This enables a controlled and sustained release of nutrients. SSF is particularly well-suited for fungi and other microorganisms that grow in low-moisture environments. However, it is unsuitable for fermenting organisms that require high water activity, such as bacteria [22]. The term solid-state fermentation applies to all forms of fermentation involving solid particles in the absence of a free liquid phase. This means the organism is grown on a bed of solid particles, with the space between the particles consisting of a continuous gas phase and liquid being retained by the solid particles, which fulfil the following three important functions: carrier material, nutrient source, and moisture reservoir. In addition to classical solid-state fermentation, various mixed forms have also become established, such as solid-substrate fermentation. Solid-state fermentation is ideal for cost-effective and substrate-optimized production of extracellular enzymes by filamentous fungi [23]. Solid-state fermentation (SSF) often uses simple, unrefined media such as grains, which may already contain all the nutrients needed for microbial growth or may only need to be moistened with a mineral solution. Pretreatment is typically minimal—usually just cooking or grinding. However, the composition and properties of these substrates can vary widely. Some products thrive only in low-moisture environments, making SSF ideal, while others require free water for microbial activity, limiting the use of SSF for their production [21].

5. Factors That Affect Enzyme Production

The production of enzymes is influenced by several key factors, including pH, temperature, substrate concentration, and metal ions. Each of these parameters plays a crucial role in determining the efficiency and yield of enzyme synthesis, especially during microbial fermentation or enzymatic reactions [2].

5.1. Effect of pH

Every enzyme functions best at a specific pH level—its optimum pH—where its activity reaches its peak. For example, pepsin operates most efficiently in highly acidic conditions (pH 1.5–2), pancreatic lipase in alkaline conditions (pH 7.5–8), and salivary amylase in slightly acidic environments (pH 6.8). Deviations from this optimal pH reduce enzymatic activity, as shifts in pH can alter the ionization states of the enzyme, the substrate, or both. In more extreme cases, such changes can even denature the enzyme, disrupting its protein structure and rendering it inactive [2]. Figure 1 shows effect of pH.

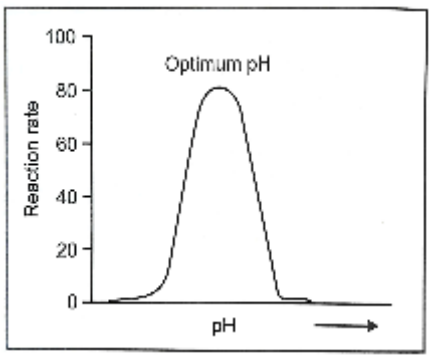

Figure 1 Effect of pH [2]

The study from Suleiman et al (2020) [24], demonstrated that pH plays a significant role in the growth and protease production of *Geobacillus thermoglucosidasius* SKF4. The bacterium exhibited optimal growth and enzyme production at pH 7 and 8, aligning with the general behavior of many *Geobacillus* species, which thrive in pH ranges of 6 to 9. pH affects microbial metabolism by influencing nutrient ionization and substrate-enzyme interactions, which in turn impacts the catalytic efficiency of protease production. Deviations from the optimal pH can lead to altered nutrient availability and reduced enzyme activity due to changes in the charge distribution of substrates and enzymes. These findings suggest that maintaining an optimal pH range is crucial for maximizing protease yield in biotechnological applications involving *G. thermoglucosidasius* SKF4 [24].

5.2. Effect of Temperature

At very low temperatures, enzymes remain inactive, but as the temperature increases, their activity gradually rises until it reaches a peak known as the optimum temperature, which in humans typically ranges from 37°C to 40°C. At this point, the enzyme functions at its highest efficiency. This increase in activity with rising temperature occurs because the higher temperature boosts the initial energy of the substrate, thereby lowering the activation energy and reducing the energy barrier for the reaction. Additionally, increased temperature enhances molecular collisions, making it more likely for molecules to interact at distances suitable for bond formation or breaking. However, if the temperature exceeds the optimum level, enzyme activity begins to decline due to denaturation [2].

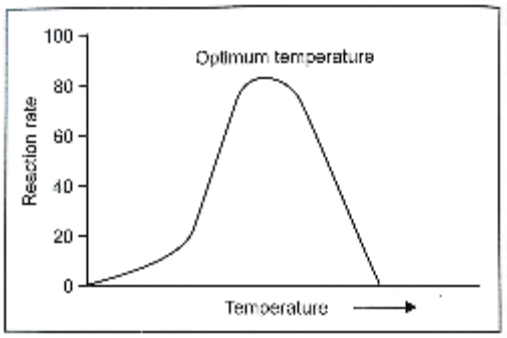

Figure 2 Effect of temperature [2]

At higher temperature (60°-65°C in human) irreversible loss of enzyme activity occurs due to denaturation of the enzymes, which are protein in nature [2]. The study from López-Trujillo et al (2023) [25] demonstrates that temperature significantly influences the production of proteolytic enzymes by *Yarrowia lipolytica* during solid-state fermentation using agro-industrial wastes. As the temperature increases, the rate of enzymatic reactions also rises, reaching an optimum point at 30 °C. At this temperature, the highest enzyme production was observed, with canola meal achieving 188.75 U/L, soybean meal 117.07 U/L, cottonseed meal 66.71 U/L, and sesame 85.51 U/L. However, beyond 30 °C, enzyme yields began to decline due to thermal stress on the microorganism, leading to reduced metabolic activity and nutrient accessibility. This result highlights 30 °C as the ideal temperature for neutral protease production by *Y. lipolytica*, emphasizing the importance of maintaining optimal thermal conditions for efficient enzyme synthesis in biotechnological applications [25].

5.3. Effect of Substrate Concentration

The rate of reaction increases as the substrate concentration increases until a certain point (V_{max}) at which the reaction attains maximal velocity. Any increase in substrate concentration after this point does not cause further increase in the rate of the reaction because at V_{max} enzyme molecules are completely saturated with substrate molecules. Figure 3 shows effect of substrate concentration.

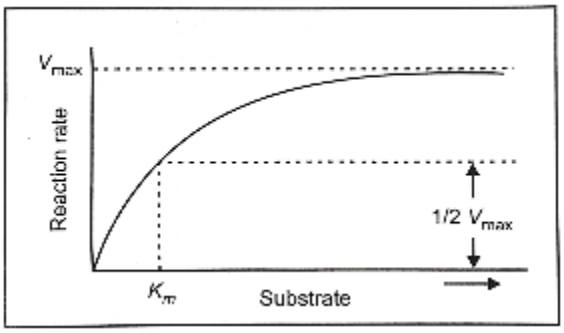

Figure 3 Effect of substrate concentration [2]

The substrate concentration that causes the reaction to proceed at its half maximal velocity (1/2 V_{max}) is called Michaelis constant (K_m). Enzymes that have low K_m, have high affinity to the substrate and act at maximal velocity at low substrate

concentration, e.g. hexokinase enzyme that acts on glucose in the fasting state (low glucose concentration). Enzymes with high K_m, have low affinity to substrate and need high concentration of substrates, e.g. glucokinase which needs high concentration of glucose so it acts maximally in the fed state [2].

According to a study Kumari et al., (2021), the activity of the soil enzyme acid phosphatase increased with rising substrate concentration up to 30 mM, after which it reached a plateau, indicating enzyme saturation. Beyond this point, further increases in substrate concentration resulted in minimal changes in activity, suggesting that all active sites of the enzyme were occupied. This behavior aligns with classical enzyme kinetics described by the Michaelis-Menten model. The kinetic parameters, V_{max} (maximum reaction velocity) and Km (Michaelis constant), were determined using three common linear transformations (Lineweaver-Burk, Hanes-Wolf, and Eadie-Hofstee), and showed consistent trends across different soil types. These findings confirm that substrate concentration significantly influences enzyme activity up to a saturation point, beyond which no further increase in reaction rate occurs due to enzyme limitation [26]

5.4. Concentration of Metal Ion Activators

The increase in metal ion activators increases the rate of enzyme action. Many enzymes are activated by metal ions, e.g. Chloride ions activate salivary amylase. Calcium ions activate thrombokinase enzyme [2]. Based on research from Tang et al (2021) [27], among the tested cations (K^+, Na^+, Ca^{2+}, Fe^{2+}, Fe^{3+}, Al^{3+}), Fe^{3+} was found to be the most effective in neutralizing HA's inhibitory effects, restoring enzymatic activity and improving hydrolysis efficiency significantly without the need for washing. This strategy presents a promising, water-conserving alternative for enhancing the bioconversion of agricultural residues, thereby supporting more economical and environmentally friendly biofuel production processes [27].

6. Catalytic Mechanisms

The catalytic mechanism of glycoside hydrolases (GHs) involves the hydrolysis of glycosidic bonds through either a retaining or inverting mechanism, depending on the enzyme's active site configuration. In retaining GHs, the reaction proceeds via a two-step double displacement mechanism involving a covalent glycosyl-enzyme intermediate, whereas in inverting GHs, a single displacement mechanism with a general acid/base catalysis leads to inversion of the anomeric configuration [28,29]. These reactions typically require two key amino acid residues: one acting as a nucleophile or base, and the other as a proton donor, often involving glutamate or aspartate residues. Structural studies and kinetic analyses have demonstrated the importance of these residues in stabilizing transition states and facilitating substrate cleavage [30,31]. Understanding these mechanisms is crucial for enzyme engineering and the development of industrial applications targeting biomass conversion and oligosaccharide synthesis.

7. Industrial Applications

Glycoside hydrolase (GH) enzymes play pivotal roles across multiple industries due to their ability to precisely modify carbohydrates such as maltooligosaccharides (MOS). In the food industry, GH enzymes like α-amylases and maltogenic amylases are used to produce MOS with prebiotic properties that promote gut health by stimulating beneficial microbiota. These enzymes are also employed in the generation of low-calorie sweeteners and in the texturization of processed foods [32]. In pharmaceuticals, the docking of GH13 enzymes with cyclodextrins is of strong pharmaceutical relevance, especially since cyclodextrins are widely used as drug solubilizers and carriers. This suggests a potential link to MOS-based drug delivery systems [33]. In biofuel and fermentation industries, GH enzymes enhance the saccharification of starch and biomass, producing fermentable sugars that improve ethanol yield and process efficiency [34]. Commercial products such as Taka-amylase A (a glucoamylase from *Aspergillus oryzae*) exemplify the industrial application of GH enzymes in MOS production [35,36]. Case studies have demonstrated the use of thermostable α-amylases in high-temperature starch liquefaction and saccharification steps, significantly boosting the economic viability of bioconversion processes. These examples highlight the versatility of GH enzymes in transforming carbohydrate-based substrates into high-value bioactive and functional compounds [37].

Industrial enzymes—highly specific biocatalysts optimized through advances in protein engineering and directed evolution—are revolutionizing numerous sectors by replacing traditional chemical catalysts with greener, more efficient processes. Engineered enzymes are increasingly used for biomass conversion to biofuels, pharmaceutical synthesis, fine chemicals production, and detergent formulation due to enhanced stability, specificity, and environmental benefits [38]. More recently, customized laccases from marine actinomycetes have demonstrated the capability to accelerate polyethylene biodegradation, achieving a ~9% breakdown in just 30 days—about six times faster than controls—offering a promising eco-friendly route for tackling persistent plastic pollution [39].

8. Challenges and Future Perspectives

Despite the widespread application of glycoside hydrolase (GH) enzymes in maltooligosaccharide (MOS) production, several challenges remain in optimizing their efficiency, stability, and specificity for industrial use. Current limitations include the narrow substrate range, suboptimal activity under extreme pH or temperature conditions, and the cost of enzyme production and purification. Future directions involve integrating synthetic biology and bioprocess optimization to develop robust, low-cost, and eco-friendly GH enzyme systems tailored for large-scale MOS production [40,41]

9. Conclusion

Amylolytic enzymes from GH families play a central role in maltooligosaccharide biosynthesis, offering environmentally friendly and substrate-specific alternatives to conventional chemical methods. The GH enzyme families exhibit diverse catalytic behaviors suited to various industrial needs, with microbial sources being particularly advantageous due to scalability and engineering potential. While both submerged and solid-state fermentation provide viable production strategies, optimizing factors such as pH, temperature, substrate concentration, and metal ion presence is crucial for maximizing yield. Despite the promising industrial applications, current limitations—such as suboptimal stability in extreme conditions and production costs—highlight the need for advanced enzyme engineering and bioprocess integration. Future innovations in synthetic biology and fermentation technology are expected to overcome these barriers, paving the way for efficient and sustainable MOS production.

Compliance with ethical standards

Disclosure of conflict of interest

No conflict of interest to be disclosed.

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