



BIOTECHNOLOGICAL POTENTIAL AND ENZYMES PRODUCED BY ACTINOBACTERIA FROM SEMI-ARID SOILS

João Moreira de Matos Neto¹, Leonardo Lima Bandeira², Ariel de Figueiredo Nogueira Mesquita¹, Suzana Claudia Silveira Martins³, Claudia Miranda Martins³.

1. Bachelor's Degree in Biotechnology (undergraduate) – Federal University of Ceará. neto.j2802@gmail.com
2. Graduate Student - Ecology and Natural Resources - Federal University of Ceará
3. Professor in the Biology Department - Federal University of Ceará

Recebido em: 15/11/2022 – Aprovado em: 15/12/2022 – Publicado em: 30/12/2022
DOI: 10.18677/EnciBio_2022D12

ABSTRACT

Soil bacteria are known to be potential degraders of plant biomass, macromolecules, and complex polysaccharides such as xylan and cellulose. Among these microbes, actinobacteria produces various extracellular enzymes, which makes this phylum a major part of the soil microbial population responsible for the decomposition of various biomolecules. In general, the members of this phylum have unique structural and reproductive aspects within the Bacteria domain, such as the colony arrangement in branched hyphae, which integrate a radial mycelium, and reproduction via sporulation. Known as 'biofactories of enzymes', actinobacteria have applications as biorefineries, in pulp and paper industry, food, agriculture, pharmaceutical uses, and many others. Actinobacteria from extreme environments such as the semi-arid region of Brazil can also produce enzymes with novel properties such as substrate specificity and stability. Actinobacteria with the potential to be applied in biotechnological industries must have a large number of enzymes. These metabolic enzymes of laccase, lipase, cellulase, and amylase from these microbes provide the potential for production and uphold the industrial requirements for societal benefit and commercialization. This review highlights the structures of actinobacteria enzymes, basic concepts about this bacterial phylum, and biotechnology with particular attention to industrially relevant enzymes.

KEYWORDS: Amylase, cellulase, laccase, *Streptomyces*, white biotechnology.

POTENCIAL BIOTECNOLÓGICO E ENZIMAS PRODUZIDAS POR ACTINOBACTÉRIAS DE SOLOS SEMI-ÁRIDOS

RESUMO

As bactérias do solo são conhecidas por serem potenciais degradadores de biomassa vegetal, macromoléculas e polissacarídeos complexos como xilana e celulose. Dentre esses microrganismos, as actinobactérias produzem diversas enzimas extracelulares, o que torna este filo a maior parte da população microbiana do solo responsável pela decomposição de diversas biomoléculas. Em geral, os membros deste filo apresentam aspectos estruturais e reprodutivos únicos dentro do domínio Bactéria, como o arranjo das colônias em hifas ramificadas, que integram um micélio radial, e a reprodução por esporulação. Conhecidas como "biofábricas de enzimas", as actinobactérias têm aplicações como biorrefinarias, na indústria de celulose e papel, alimentos, agricultura, usos farmacêuticos e muitos outros. Actinobactérias de ambientes extremos, como a região semiárida do Brasil, também

podem produzir enzimas com novas propriedades, como especificidade e estabilidade do substrato. Actinobactérias com potencial para serem aplicadas em indústrias biotecnológicas devem possuir um grande número de enzimas. Essas enzimas metabólicas de lacase, lipase, celulase e amilase desses micróbios fornecem o potencial de produção e sustentam os requisitos industriais para benefício e comercialização da sociedade. Esta revisão destaca as estruturas das enzimas de actinobactérias, conceitos básicos sobre este filo de bactérias e biotecnologia com atenção especial para enzimas industrialmente relevantes.

PALAVRAS-CHAVE: Amilase, biotecnologia branca, celulase, lacase, *Streptomyces*

INTRODUCTION

Several studies have reported different solutions for industrial demands in terms of processes. Microorganisms with multifunctional traits are among the proposed solutions and have been found to, among many things, reduce the use of chemical fertilizers and pesticides by producing or releasing different types of bioactive enzymes, compounds, antimicrobial substances or biocontrol compounds (LIU *et al.*, 2018; KHOSHRU *et al.*, 2020).

The use of enzymes, which are catalysts that increase reaction rates of biological processes, has gained prominence in several industrial segments as an alternative to conventional methods (PINHEIRO *et al.*, 2021). The global enzyme market was valued at almost US\$10 billion in 2019 and is expected to increase at an annual rate. The growing interest in these biocatalysts compared to chemical catalysts can be attributed to their high specificity, the ability to operate under low energy consumption, mild temperature and pH conditions, and their positive environmental impact (GIRELLI *et al.*, 2020).

Actinobacteria can be the answer for this increasing industrial enzyme production, since they produce several biologically active and important secondary metabolites, such as anti-tumor, antimicrobial and antiviral compounds (PHAM *et al.*, 2019). Several actinobacteria have been reported to produce enzymes of industrial interest, such as proteases, amylases, and cellulases, but not only this but this bacterial phylum can also produce other enzymes such as lignin and laccase, which have had potential use for biotechnological purposes (GOHAIN *et al.*, 2020). Enzymes obtained from actinobacteria have high stability, availability, and productivity. Not only this, but are also low cost, have a sustainable production and are practical and ecofriendly, which makes them a great industry investment (FERREIRA *et al.*, 2020).

Regarding these enzymes, microbial cellulase plays a role in environmental issues. The actual trend in the cellulase market is genome mediated application of cellulase production by actinobacteria through the recombination technology (SAHOO *et al.*, 2019). Amylases can be applied as an additive in the detergent industry and also in the production of maltose syrup and biodegradation of food waste (KHAROUF *et al.*, 2021). Xylanases, as well as pectinases, can be used in the clarification of juices, production of bioethanol, in the bakery industry as an additive and in paper bleaching (WALIA *et al.*, 2017).

From this perspective, actinobacteria are a source of these enzymes with desirable characteristics. Therefore, this review seeks to show a little about these microorganisms, biotechnology, and how these enzymes are structured.

Biotechnology concept

Defined as the science of manipulating organisms, organic systems and processes in order to generate a social, environmental or industrial benefit,

Biotechnology has been growing and establishing itself in the recent years. This is an area that was first consolidated in the United States and that has recently been established in underdeveloped and developing countries, as is the case in Brazil (BARCELOS *et al.*, 2018).

As it is a highly plural and interdisciplinary field of knowledge, many problems have been associated with the definition of biotechnology since it was first mentioned by Karl Erkey in 1919, with its concept undergoing several changes over the decades (VERMA *et al.*, 2011).

To facilitate the understanding of the plurality of this area, Kafarski (2012) developed a color scheme associated with the areas of activity and application of biotechnology. The colors and their respective contexts are as follows:

- Yellow: Nutritional biotechnology is one of the oldest branches of biotechnology, whose main focus is food production. Important advances in this area are being made in order to improve food characteristics, with the modification of specific nutritional factors, increasing the availability of vitamins, or decreasing the presence of allergens, for example.

- Blue: Marine biotechnology is based on the study and application of natural resources from marine sources. The pelagic environment is a remarkable source of bioactive compounds of biotechnological interest, where algae, microalgae and other microorganisms present in it stand out. This area intersects with several other areas of biotechnology, since marine biotechnology can generate inputs applicable to several other branches of biotechnology.

- White: Industrial Biotechnology is based on the application of biocatalysts to industrial processes. The focus was on the replacement of traditional industrial processes, the production of specific action biopolymers, the production of alternative biofuels to fossil fuels and production of enzymes or microorganisms relevant to the industry. White biotechnology is considered to be the largest of the biotechnological domains and has special relevance within the area, directly competing with classic technologies.

- Grey: Environmental Biotechnology aims at solving problems of environmental interest, such as the treatment of industrial effluents, phytoremediation or bioremediation based on microorganisms from polluted areas, reuse of waste and recovery of degraded soils.

- Golden: Bioinformatics, Nanotechnology and Systems Biology.

- Brown: Biotechnology of deserts and arid zones, which is related to the management of natural resources in dry regions, where resource management is a critical point for the resident populations of these regions. Biotechnology, in this case, becomes a tool to help face the adversities found in arid zones, and can be used in the development of cultivars resistant to high soil salinity, with low water demands and resistant to phytopathogens.

- Black: Regards Bioterrorism and Biological Weapons. Not all aspects of biotechnology have a direct positive impact, as is the case of black biotechnology, which uses biotechnological tools to produce biological weapons.

- Green: Biotechnology applied to agriculture is considered the new phase of the green revolution. It uses biotechnological techniques to develop more fertile cultivars that are more resistant to biotic and abiotic stresses. This area also encompasses modern applications of biotechnology, such as micropropagation techniques and genetic engineering for the development of plants with artificially selected specific characteristics.

- Red: Biotechnology applied to health is involved with the preservation of human health, encompassing the production of new drugs, vaccines and antibiotics, as well as the development of new regenerative therapies, synthetic organs, and new diagnostic methods.

- Violet: Represents Biotechnology Associated with Legislation and Bioethics. As biotechnology has become a constant concern in people's lives, both from the ethical-legislative point of view and from the layman's point of view, violet biotechnology emerged as a response to these problems, focused mainly on the discussion and resolution of such problems.

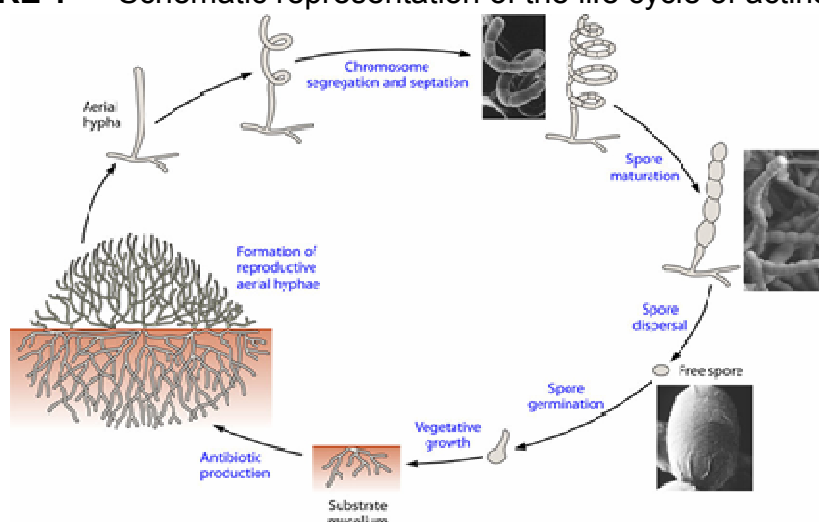
However, the author insists on emphasizing that the color system is incomplete, since biotechnology is an area in constant evolution and that new areas of knowledge can be developed and adapted to the schematization.

Actinobacteria

Actinobacteria or actinomycetes, as previously known, are Gram-positive filamentous prokaryotic microorganisms that have a high proportion ($\geq 55\%$) of guanine (G) and cytosine (C) in their genome (SEGARAN *et al.*, 2017). These microorganisms make up the largest and most taxonomically diverse phylum of the Eubacteria kingdom: the Actinobacteria phylum, which comprises a total of 23 orders and, until December 2015, 342 genera (EL OTHMANY *et al.*, 2021).

In general, members of this phylum have unique structural and reproductive aspects within the Bacteria domain (Figure 1), such as colony arrangement in branched hyphae, which integrate a radial mycelium, and reproduction via sporulation. Such characteristics are similar to those of filamentous fungi; however, at the cellular level, the cells that make up the hyphae have typical aspects of Gram-positive prokaryotic organisms: absence of a true nucleus, presence of chromosome organized in bacterial nucleoid, regions of cytoplasmic DNA, and presence of peptidoglycan cell wall. In the latter case, there is the exception of members of the order Corynebacteriales, where there is the development of a membrane external to the bacterial cell wall (LI *et al.*, 2016; RAHLWES; SPARKS; MORITA, 2019).

FIGURE 1 - Schematic representation of the life cycle of actinobacteria.



Source: Adapted from Barka *et al.*, (2016).

Given the structural characteristics of actinobacteria, the mycelium formed by the grouping of actinobacterial hyphae can generally be subdivided into three main types: vegetative or substrate mycelium, aerial mycelium, and reproductive mycelium

or spore-bearing mycelium (LI *et al.*, 2016). Despite these generalist definitions, it is important to point out that not all genera and species are fully adequate to the described characteristics, considering that only some of these are capable of effectively forming all the described structures.

Actinobacteria are intimately involved in key ecological functions, acting mainly as saprophytes: organic matter degrading beings that aid the return of carbon to its biogeochemical cycle (NALINI; PRAKASH, 2020). Furthermore, these prokaryotes are able to act as regulator to other microbial populations through the production of secondary metabolites that can perform antagonistic or symbiotic relations between others microorganism (RIBEIRO *et al.*, 2022), insects (RODRÍGUEZ-HERNÁNDEZ *et al.*, 2019) or plants, in this last quote, through the production of plant growth regulators or other type of vegetal hormones (BOUKHATEM *et al.*, 2022).

This actinobacterial metabolic robustness is needed to effectively perform so many functions and inhabit a range of environments, including those which possess extreme conditions: high salinity, high temperatures, high solar irradiation and low nutrient or water availability (SIVAKALA *et al.*, 2021) is what justifies their wide enzymatic potential and their vast number of produced bioactive molecules. Thus, actinobacteria are one of the most studied sources of composts of biotechnological interest, responsible for two thirds of all biotic related antibiotics (KALTENPOTH, 2009) and being widely studied as founts of secondary metabolites (HASSAN *et al.*, 2019; SALWAN; SHARMA, 2020), enzymatic inhibitors (SIDDHART *et al.*, 2019) and enzymes (ALVES *et al.*, 2016; ROMEU *et al.*, 2021; ELFRAMAWY *et al.*, 2022).

The vegetative mycelium is slender, transparent and highly branched, being the first structure formed from the germination of the dispersed form of the reproductive spores of another colony. It is responsible for the secretion of extracellular enzymes, absorption of nutrients presents in the medium and attachment of the colony to the substrate. (HAZARIKA; THAKUR, 2020). At a certain point in the life cycle of the actinobacterial colony, the vegetative mycelium tends to emerge from the substrate and form the so-called aerial mycelium. This mechanism is mainly triggered by the decrease in the availability of nutrients in the environment and characterized by the sudden change in the general characteristics of the hyphae, especially in their hydrophobicity characteristics.

Enzymes

Enzymes are lytic biomolecules of a mostly protein nature, responsible for key metabolic functions in any existing biological system. The performance of their metabolic charges is due to the ability of these macromolecules to recognize specific substrates and decrease the activation energy of the reactions that convert substrates into products and vice versa. The enzyme catalysis reaction is carried out through the joint action of two peptide portions of the enzymes: the binding site and the catalysis site. The binding site is responsible for the specificity of the binding of enzymes to their specific substrates and analogs, while the portion of the catalysis site is the peptide characterized by the presence of specific groups or ions that will be responsible for performing actual conversion reactions (VITOLO, 2020).

The International Enzyme Commission (IEC) has classified a total of six major classes of enzymes according to the type of reaction catalyzed: Oxidoreductases [EC-1], Transferases [EC-2], Hydrolases [EC-3], Lyases [EC-4], Isomerases [EC-5] and Ligases [EC-6] (MOJSOV, 2012). Among these six classes, the hydrolases group has a certain prominence, since it brings together enzymes capable of using water molecules to carry out covalent bond breaking reactions, demonstrating unique importance in a physiological context, since they are responsible for the conversion

of nutrients to monomeric or oligomeric subunits that are more easily used by the organism and, due to the need for broad action, end up having a lower specificity to substrates (HOYO *et al.*, 2017).

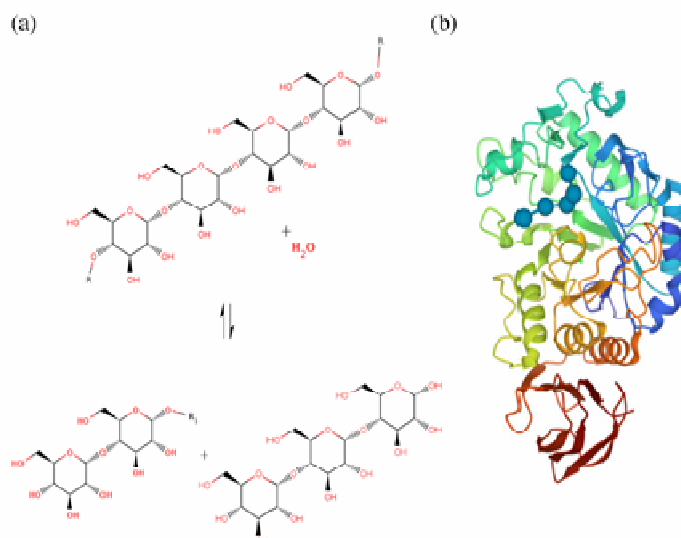
Capable of performing countless biological processes, enzymes are considered biomolecules of unparalleled biotechnological importance, subject to applications in almost all areas, such as agriculture, industry, environment, and health. The biotechnological interest involving these enzymes ends up turning more strongly to microbial sources, since microbial enzymes have less time and cost for production, higher yields and greater stability under extreme conditions. Furthermore, many microorganisms end up secreting several enzymes directly into the culture medium, which facilitates the downstream processes (GOPINATH, 2017).

Amylases

Starch is a glucose biopolymer resulting from the mixture of two other polysaccharides: amylose (α -1,4 bonds) and amylopectin (α -1,4 and α -1,6 bonds). This molecule is one of the main sources of energy for living beings and is produced and metabolized by different organisms. With the starch hydrolysis being mediated through the production of hydrolytic enzymes called amylases, which are subdivided into three groups: γ -Amylases, β -Amylases and α -Amylases [EC-3.2.1.1], the latter group being known to have a higher reaction rate compared to the other two.

Also known as glycosyl hydrolases, because the glycosidic bonds are their hydrolysis focus, these enzymes can be subdivided into two other subgroups depending on the site of enzymatic action on the starch molecules. Endoamylases hydrolyze the starch molecule randomly, forming oligosaccharides of different characteristics, while exoglucanases act only on the ends of the polysaccharide chains, forming D-glucose (monosaccharide) and Maltose (Disaccharide). (GOPINATH, 2017). The mechanism of starch hydrolysis mediated by α -Amylases and an example structure can be found in Figure 2.

FIGURE 2 – (a) Mechanism of action of starch hydrolysis mediated by α -Amylase (BRENDA) (b) Three-dimensional structure of α -Amylase isolated from *Bacillus subtilis* (RCSB PDB accession code: 1BAG).



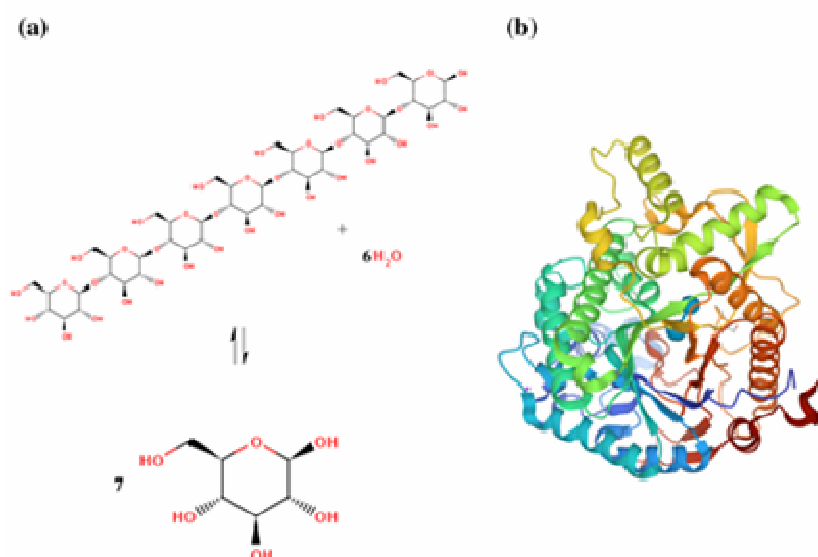
Source: Authors, (2022).

These hydrolases have diverse applications, capable of being applied in the food industry, in the starch conversion industry, in the detergent industry and in the pulp and paper industry (FAROOQ, 2021). In addition, the by-products of starch hydrolysis has several applications, especially in the food industry, where they are used as sweeteners, thickeners, gels, and texture controllers (WHISTLER; DANIEL, 2000).

Cellulases

Considered the most abundant biopolymer on earth, cellulose is a polysaccharide of D-glucose (β -1,4 bonds), characterized by the formation of an arrangement in crystalline microfibrils that conjugate to form the cellulose fiber. Due to these characteristics (disposition of microfibrils and type of glycosidic bond), cellulose is not a macromolecule easily metabolized by a good portion of living organisms, requiring a total of three enzymatic types for its total degradation: β -glucosidases [EC-3.2. 1.21], exoglucanases [EC-3.2.1.91] and endoglucanases [EC-3.2.1.4] (BEHERA; RAY, 2016). The main organisms responsible for its catalysis are of microbial origin, such as filamentous fungi (VIETO *et al.*, 2022), yeasts (SOHAIL *et al.* 2022) and bacteria (MSANGOSOKO *et al.*, 2021), mainly actinobacteria (ZAKALYUKINA *et al.*, 2021; SHARMA *et al.*, 2022). Elucidation of the mechanism of action and a structural example of β -glucosidase can be found in Figure 3.

FIGURE 3 - (a) Mechanism of action of β -glucosidase-mediated hydrolysis mediated by β -glucosidase (BRENDA) (b) Three-dimensional structure of β -glucosidase isolated from *Neotermes koshunensis* (RCSB PDB accession code: 3VIK).



Source: Authors, (2022).

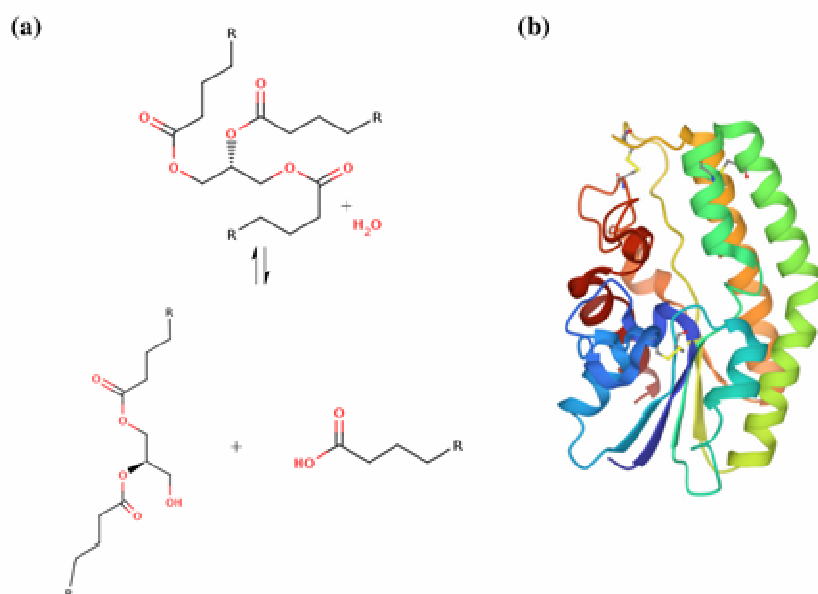
Cellulolytic enzymes and microorganisms that produce these enzymes, in general, have diverse biotechnological applications, such as in agriculture (SILVA *et al.*, 2019), in waste treatment (SHARMA; KUMAWAT; KAUR, 2022), and in industries, such as detergents, pulp and paper, textiles, and in the fermentation of biomass into biofuels (KUMARI *et al.*, 2019; RAJKUMAR *et al.*, 2021).

Lipases

Lipids are diverse biomolecules that play fundamental roles in metabolic homeostasis. These molecules can act as a source of cellular energy, molecular signals, membrane components, among many other functions. In summary, lipids are nonpolar biomolecules, insoluble in water, and soluble in organic solvents. This class of molecules includes: triacylglycerols, defined as esters formed by the union of one glycerol molecule with three other fatty acids, which in turn are classified as long-chain hydrocarbons that may or may not have unsaturations in their chains, with such unsaturations can be classified as *cis* or *trans* depending on their conformations; ester waxes, which are simple fatty acid molecules esterified to a fatty alcohol molecule; phospholipids, defined as two fatty acids esterified to an L-Glycerol-3-phosphate; phosphosphingolipids, molecules similar to phospholipids, but which have an amino alcohol (sphingosine) esterified to a long-chain fatty acid; and sterols (SARGENT *et al.*, 2003; AHMED *et al.*, 2020;).

Lipases or triacylglycerol lipases [EC-3.1.1.3], in turn, are enzymes capable of degrading this diverse class of biomolecules. The mechanism of action associated with the lipase-mediated hydrolysis reaction of triacylglycerols and a structural example of a lipase are illustrated in Figure 4.

FIGURE 4- (a) Mechanism of action of triacylglycerol lipase-mediated hydrolysis of triacylglycerol (BRENDA) (b) Three-dimensional structure of lipase isolated from *Streptomyces rimosus* (RCSB PDB accession code: 5MAL).



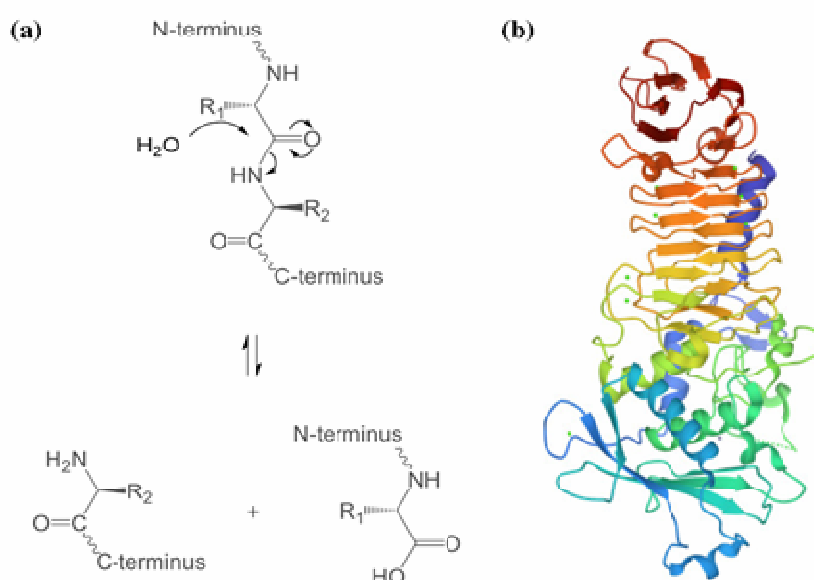
Source: Authors, (20220).

These enzymes hydrolyze esterified, transesterified and inter-esterified regions, being extremely versatile and applicable from a biotechnological point of view, and can be used in the production of biofuels (RACHMADONA *et al.*, 2020 ; CONSTANTINI; CALIFANO, 2021), as biosensors (HASANAH *et al.*, 2019), in the leather industry (MOUJEHED *et al.*, 2022; LI *et al.*, 2020), in the treatment of industrial effluents (RACHMADONA *et al.*, 2020), in the textile industry (EL MENOIFY *et al.*, 2022), in the oil, aroma and flavor, pharmaceutical industry (VANLEEuw *et al.*, 2019), among many others.

Proteases

Proteases or peptidases [EC-3.4] are an enzymatic subclass of the group of hydrolases that perform the cleavage of C-N bonds involving two amino acids (peptide bonds) in proteins and peptides. This class of enzymes, although quite unique in terms of functionality, presents a certain structural plurality when analyzing its catalysis mechanisms (nucleophiles), thus they can be divided into six classes: serine peptidases [EC-3.4.21], glutamyl peptidases [3.4.21.19], cysteine peptidases [EC-3.4.22], aspartate peptidases [EC-3.4.23], metallopeptidases [EC- 3.4.24] and threonine peptidases (RAWLINGS; BATEMAN, 2019). The reaction mechanism of peptidases and a structural example can be found in Figure 5.

FIGURE 5 - (a) Reaction scheme of peptidases-mediated proteolysis hydrolysis (BRENDA) (b) Three-dimensional structure of psychrophilic protease isolated from *Pseudomonas* sp. (RCSB access code: 1H71).



Source: Authors, (2022).

These enzymes have a wide variety of biotechnological applications: representing one of the three largest groups of industrial enzymes, accounting for approximately 60% of enzyme world's income in the commercialization (MAMO; ASSEFA, 2018), a sector that is expected to reach a commercial value of approximately \$9.10 billion by the end of 2026 (Industrial Enzymes Market, 2022), subject to application in the beverage industry (CHOI *et al.*, 2019; LIM *et al.*, 2022), in the detergent industry as bioadditives (SALWAN; SHARMA, 2019), in the cheese industry as milk coagulants (ALAVI; MOMEN, 2020), in the meat industry as tenderizers (GAGAOUA *et al.*, 2021), in the cosmetics industry (VIDMAR; VODOVNIK, 2018), in effluent treatment (RAMAKODI *et al.*, 2020), as bioremediation molecules (KUMAR; JAIN, 2020), as a food supplement (WANG *et al.*, 2020), as well as countless other uses.

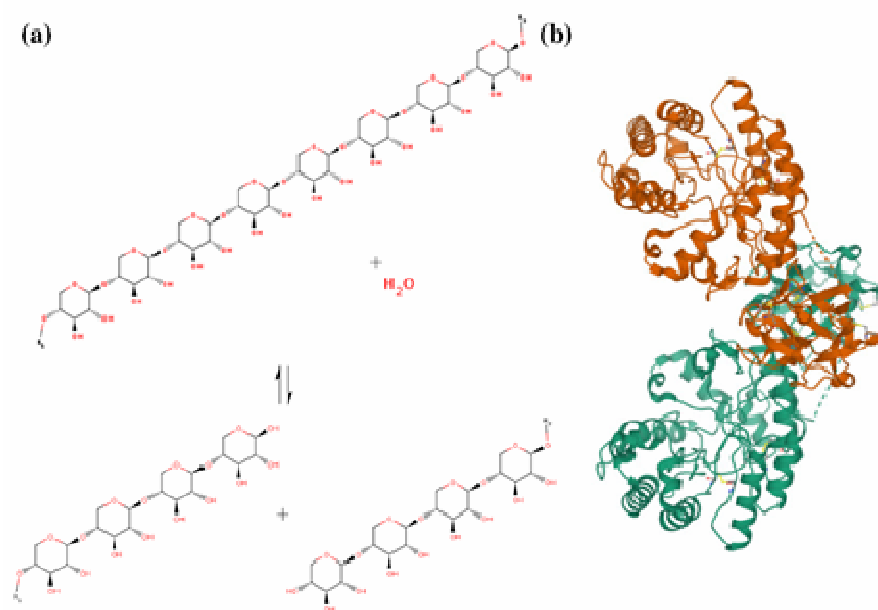
Xylanases

Xylan is the most abundant hemicellulose present in the cell walls of plants and algae and can make up about 30% of the dry mass of terrestrial plants. This

polysaccharide consists of a backbone of D-xylose subunits joined by β -1,4 glycosidic bonds, which can be variable in terms of structure, being able to present itself as a purely linear polyxylose backbone, or as a heteropolysaccharide of diverse structure (BAJPAI, 2014).

Therefore, xylanases or xylanhydrolases [EC-3.2.1.8] are the main enzymes responsible for the xylan degradation process, that is, they are hydrolytic agents of β -1,4 glycosidic bonds (HECK *et al.*, 2005). The reaction mechanism of endoxylanases and a structural example can be found in Figure 6.

FIGURE 6 - (a) Reaction scheme for endoxylanase-mediated xylan hydrolysis (BRENDA) (b) Three-dimensional structure of endoxylanase isolated from *Streptomyces olivaceoviridis* (RCSB accession code: 1XYF).



Source: Authors, (2022)

The biotechnological potential associated with these enzymes is very broad, since xylan is a material of high bioavailability and can be used for the production of biofuels (BIBRA *et al.*, 2018; SHARMA *et al.*, 2020), in the industry of paper as a bleaching agent of biological origin (MHIRI *et al.*, 2020), in the food industry as a juice clarifier (ADIGUZEL *et al.*, 2019), as a poultry feed supplement (SINGH *et al.*, 2021), in the bread and wheat industry (BOTH *et al.*, 2021) and many others.

Laccases

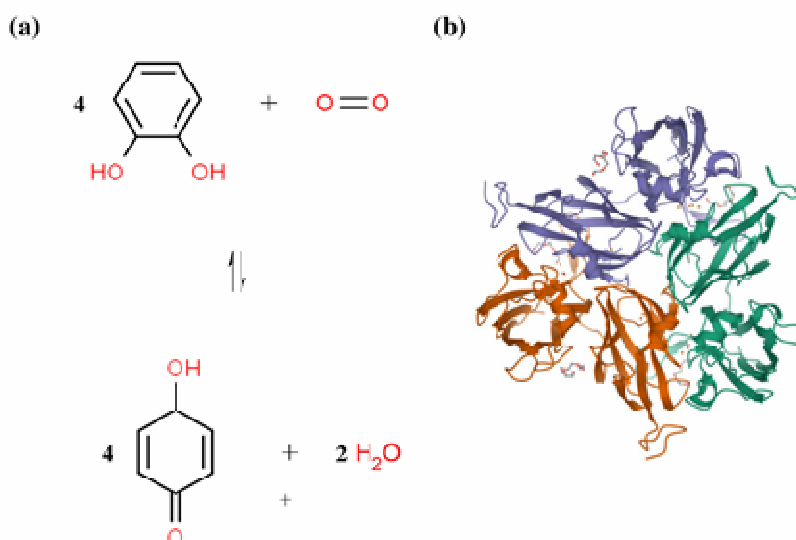
Laccases [EC-1.10.3.2], unlike all the other enzymatic classes mentioned, are not part of the group of hydrolases, but of the oxidoreductases, enzymes that catalyze the oxidation-reduction reaction in their substrates. In general, the laccase group encompasses lytic proteins that carry copper ions in their structure, being members of an enzymatic family called multicopper oxidases (MCOs), capable of oxidizing a wide range of substrates using oxygen gas molecules (O_2) as the final electron acceptor, reducing it to H_2O without releasing partially reduced by-products called reactive oxygen species (ROS). Laccases are capable of performing catabolic and anabolic nature, acting on the degradation of humus and lignin, in the synthesis of

polymeric pigments, in the lignification process, in the synthesis of polyflavonoids and in the humidification of soil organic matter (JANUSZ *et al.*, 2020).

Although the enzymes that make up this enzymatic group have structural similarity to each other, they differ in regard to their redox potential. Laccases with high redox potential have a wider spectrum of action and are therefore more attractive from a biotechnological point of view (SUN *et al.*, 2021). It is possible to observe that a good part of low redox potential laccases can be found in plants, animals and bacteria, whereas enzymes of the same family with high redox potential are found mostly in fungi (MUNK *et al.*, 2015), but can also be found in other organisms, such as actinobacteria (TRUBTSINA *et al.*, 2021).

The high bioremediation capacity that these enzymes have, especially in the degradation of azo dyes in the textile industry, makes this one of the main focuses of studies involving biotechnological applications of laccases (GOUD *et al.*, 2020; TRUBTSINA *et al.*, 2021; ADESANYA; ADESANYA, 2022). However, this does not exclude other applicability, as in humidification and composting (LI *et al.*, 2022), in the production of anticancer drugs, antioxidant hormone drugs, biosensors, and food product stabilizers (SENTHIVELAN *et al.*, 2016; KAUR *et al.*, 2022). Examples of a laccase-catalyzed reaction scheme and a three-dimensional model of this enzyme can be found in Figure 7.

FIGURE 7 - (a) Laccase-mediated oxidation-reduction reaction of benzenediol to benzosemiquinone (BRENDA) (b) Three-dimensional structure of laccase isolated from *Streptomyces coelicor* (RCSB accession code: 3CG8).



Source: Authors, (2022).

FINAL CONSIDERATIONS

The growing need for stable, multipurpose biocatalysts and the expected scaling of enzymatic market highlights the need for research of novel enzymes and exploration of biotechnological potential in areas not yet thoroughly explored. Actinobacteria isolated from multiple sources were already reported to produce many lytic proteins, including the ones presented in this review. The Brazilian semi-arid region is a hotspot for this bacterial phylum and its extreme environment is

characterized by high temperatures, saline soils and low water and nutrient availability. The aforementioned information combined with actinobacteria's high adaptability and ubiquitously distribution denotes that this understudied region can act as source of those prokaryotes for high throughput enzymatic production bioprocesses, suggesting a high potential not only for white biotechnology, but from related areas as green, red and grey biotechnology.

REFERENCES

ADESANYA, A.; ADESANYA, V. A. Laboratory-Scale Study: Biodegradation of Bisphenol A (BPA) by Different Actinobacterial Consortium. In: **Actinobacteria - Diversity, Applications and Medical Aspects**, IntechOpen, 2022. DOI: 10.1016/j.procbio.2022.04.015

ADIGUZEL, G.; FAIZ, O.; SISECIOGLU, M.; SARI, B.; BALTACI, O.; *et al.*; A novel endo- β -1, 4-xylanase from *Pediococcus acidilactici* GC25; purification, characterization and application in clarification of fruit juices. **International Journal of Biological Macromolecules**, v. 129, p. 571-578, 2019. DOI: 10.1016/j.ijbiomac.2019.02.054

AHMED, S.; SHAH, P.; AHMED, O. Biochemistry, Lipids. **National Center for Biotechnology**, 2022. Disponível em: <https://www.ncbi.nlm.nih.gov/books/NBK525952/>. Acesso em: 13 de novembro de 2022.

ALAVI, F.; MOMEN, S. Aspartic proteases from thistle flowers: Traditional coagulants used in the modern cheese industry. **International Dairy Journal**, v. 107, p. 104709, 2020. DOI: 10.1016/j.idairyj.2020.104709

ALVES, D.; SILVA, V.M.; GARCIA, F.; MARTINS, S.C.; MARTINS, C. Produção de celulase e amilase por actinobactérias do semiárido brasileiro. **Enciclopédia Biosfera**, v. 13, n. 24, 2016. DOI: 10.18677/EnciBio_2016B_121

BAJPAI, P.; Chapter 2-Xylan: occurrence and structure. **Xylanolytic Enzymes**, v. 16, p. 9-18, 2014. DOI:10.1016/B978-0-12-801020-4.00002-0

BARKA, E. A.; VATSA, P.; SANCHEZ, L.; GAVEAU-VAILLANT, N.; JACQUARD, C. *et al.* Taxonomy, physiology, and natural products of Actinobacteria. **Microbiology and Molecular Biology Reviews**, v. 80, n. 1, p. 1-43, 2016. DOI: 10.1128/MMBR.00019-15

BARCELOS, M. C.; LUPKI, F. B.; CAMPOLINA, G. A.; NELSON, D. L.; MOLINA, G. The colors of biotechnology: general overview and developments of white, green and blue areas. **FEMS Microbiology Letters**, v. 365, n. 21, p. fny239, 2018. DOI: 10.1093/femsle/fny239

BEHERA, S. S.; RAY, R. C. Solid state fermentation for production of microbial cellulases: recent advances and improvement strategies. **International Journal of Biological Macromolecules**, v. 86, p. 656-669, 2016. DOI: 10.1016/j.ijbiomac.2015.10.090

BIBRA, M.; KUNREDDY, V. R.; SANI, R. K. Thermostable xylanase production by *Geobacillus* sp. strain DUSELR13, and its application in ethanol production with lignocellulosic biomass. **Microorganisms**, v. 6, n. 3, p. 93, 2018. DOI: 10.3390/microorganisms6030093

BOTH, J.; BIDUSKI, B.; GÓMEZ, M.; BERTOLIN, T. E.; FRIEDRICH, M. T. *et al.* Micronized whole wheat flour and xylanase application: dough properties and bread quality. **Journal of Food Science and Technology**, v. 58, n. 10, p. 3902-3912, 2021. DOI: 10.1007/s13197-020-04851-2

BOUKHATEM, Z. F.; MERABET, C.; TSAKI, H. Plant growth promoting actinobacteria, the most promising candidates as bioinoculants?. **Frontiers in Agronomy**, p. 14, 2022. DOI: 10.3389/fagro.2022.849911

CHOI, Y.; LIM, T.; HE, Y.; HWANG, K. T. Chemical characteristics and antioxidant properties of wheat gluten hydrolysates produced by single and sequential enzymatic hydrolyses using commercial proteases and their application in beverage system. **Journal of Food Measurement and Characterization**, v. 13, n. 1, p. 745-754, 2019. DOI: 10.1007/s11694-018-9987-x

COSTANTINI, A.; CALIFANO, V. Lipase immobilization in mesoporous silica nanoparticles for biofuel production. **Catalysts**, v. 11, n. 5, p. 629, 2021. DOI: 10.3390/catal11050629

EL OTHMANY, R.; ZAHIR, H.; ELLOUALI, M.; LATRACHE, H. Current Understanding on Adhesion and Biofilm Development in Actinobacteria. **International Journal of Microbiology**, v. 2021, 2021. DOI: 10.1155/2021/6637438

EL MENOIFY, H. A.; GOMAA, S. K.; HAROUN, A. A.; FARAG, A. N.; SHAFEI, M. S. *et al.* Comparative studies of free and immobilized partially purified lipase from *Aspergillus niger* NRRL-599 produced from solid-state fermentation using gelatin-coated titanium nanoparticles and its application in textile industry. **Egyptian Pharmaceutical Journal**, v. 21, n. 2, p. 143, 2022. DOI: 10.4103/epj.epj_90_21

ELFRAMAWY, A.; EL-HANAFY, A.; SHARAMANT, M.; GHOZLAN, H. Molecular identification of native Egyptian Actinobacteria: Screening for lignin utilization and degradation of lignin model compounds. **Biocatalysis and Agricultural Biotechnology**, v. 40, p. 102289, 2022. DOI: 10.1016/j.bcab.2022.102289

FERREIRA, J. S.; OLIVEIRA, D.; MALDONADO, R. R.; KAMIMURA, E. S.; FURIGO, A. Enzymatic pretreatment and anaerobic co-digestion as a new technology to high-methane production. **Applied microbiology and Biotechnology**, v. 104, n. 10, p. 4235-4246, 2020. DOI: 10.1007/s00253-020-10526-x

GAGAOUA, M.; DIB, A. L.; LAKHDARA, N.; LAMRI, M.; BOTINEȘTEAN, C. *et al.* Artificial meat tenderization using plant cysteine proteases. **Current Opinion in Food Science**, v. 38, p. 177-188, 2021. DOI: 10.1016/j.cofs.2020.12.002

GIRELLI, A. M.; ASTOLFI, M. L.; SCUTO, F. R. Agro-industrial wastes as potential carriers for enzyme immobilization: A review. **Chemosphere**, v. 244, p. 125368, 2020. DOI: 10.1016/j.chemosphere.2019.125368

GOHAIN, A.; MANPOONG, C.; SAIKIA, R.; DE MANDAL, S. Actinobacteria: diversity and biotechnological applications. **Recent Advancements in Microbial Diversity**, p. 217-231, 2020. DOI: 10.1016/B978-0-12-821265-3.00009-8.

GOPINATH, S. C.; ANBU, P.; ARSHAD, M. M.; LAKSHMIPRIYA, T.; VOON, C. H. *et al.* Biotechnological processes in microbial amylase production. **BioMed Research International**, v. 2017, 2017. DOI: 10.1155/2017/1272193

GOUD, B. S.; CHA, H. L.; KOYYADA, G.; KIM, J. H. Augmented biodegradation of textile azo dye effluents by plant endophytes: a sustainable, eco-friendly alternative. **Current Microbiology**, v. 77, n. 11, p. 3240-3255, 2020. DOI: 10.1007/s00284-020-02202-0

HASANAHA, U.; SANI, N. D. M.; HENG, L. Y.; IDROES, R.; SAFITRI, E. Construction of a hydrogel pectin-based triglyceride optical biosensor with immobilized lipase enzymes. **Biosensors**, v. 9, n. 4, p. 135, 2019. DOI: 10.3390/bios9040135

HASSAN, Q. P.; BHAT, A. M.; SHAH, A. M. Bioprospecting actinobacteria for bioactive secondary metabolites from untapped ecoregions of the northwestern Himalayas. In: **New and Future Developments in Microbial Biotechnology and Bioengineering**. Elsevier, 2019. p. 77-85. DOI: 10.1016/B978-0-444-63504-4.00006-2

HAZARIKA, S. N.; THAKUR, D. ACTINOBACTERIA. In: **Beneficial Microbes in Agro-Ecology**. Academic Press, 2020. p. 443-476. DOI: 10.1016/B978-0-12-823414-3.00021-6

HECK, J. X.; FLÔRES, S. H.; HERTZ, P. F.; AYUB, M. A. Z. Optimization of cellulase-free xylanase activity produced by *Bacillus coagulans* BL69 in solid-state cultivation. **Process Biochemistry**, v. 40, n. 1, p. 107-112, 2005..

HOYOS, P.; HERNÁIZ, M. J.; ALCÁNTARA, A. R. 3.28-Biocatalyzed production of fine chemicals. In: **Comprehensive Biotechnology**. Pergamon Oxford, 2017. p. 334-373. DOI: 10.1016/b978-0-08-088504-9.00225-7

Industrial Enzymes Market by Type (Carbohydrases, proteases, Lipases, Polymerases & Nucleases), Application (Food & Beverages, Bioethanol, Feed, Detergents, Wastewater, Soil, and Oil Treatment), Source, Formulation and Region – Global Forecast to 2026, **Markets and Markets**, 2022. Disponível em: <https://www.marketsandmarkets.com/Market-Reports/industrial-enzymes-market-237327836.html> . Acesso em: 30 de out. De 2022.

JANUSZ, G.; PAWLIK, A.; ŚWIDERSKA-BUREK, U.; POLAK, J.; SULEJ, J. *et al.* Laccase properties, physiological functions, and evolution. **International Journal of Molecular Sciences**, v. 21, n. 3, p. 966, 2020. DOI: 10.3390/ijms21030966

KAFARSKI, P. Rainbow code of biotechnology. **Chemik**, v. 66, n. 8, p. 811-816, 2012.

KALTENPOTH, M. Actinobacteria as mutualists: general healthcare for insects?. **Trends in microbiology**, v. 17, n. 12, p. 529-535, 2009. DOI: 10.1016/j.tim.2009.09.006

KAUR, R.; SALWAN, R.; SHARMA, V. Structural Properties, Genomic Distribution of Laccases from *Streptomyces* and Their Potential Applications. **Process Biochemistry**, 2022. DOI: 10.1016/j.procbio.2022.04.015

KHEROUF, M.; HABBECHÉ, A.; BENAMIA, F.; SAOUDI, B.; KEROUAZ, B. *et al.* Statistical optimization of a novel extracellular alkaline and thermostable amylase production from thermophilic *Actinomadura keratinilytica* sp. Cpt29 and its potential application in detergent industry. **Biocatalysis and Agricultural Biotechnology**, v. 35, p. 102068, 2021. DOI: 10.1016/j.bcab.2021.102068

KHOSHROU, B.; MOHARRAMNEJAD, S.; GHARAJEH, N. H.; LAJAYER, B. A.; GHORBANPOUR, M. Plant microbiome and its important in stressful agriculture. In: **Plant Microbiome Paradigm**. Springer, Cham, 2020. p. 13-48. DOI: 10.1007/978-3-030-50395-6_2

KUMAR, L.; JAIN, S. K. Role of Proteases in Bioremediation of Temple Protein-Containing Waste with Special Reference to Mangalnath, Ujjain (MP)–India. **Indian Journal of Pure and Applied Biosciences**, v. 8, n. 3, p. 602-607, 2020. DOI: 10.18782/2582-2845.8178

KUMARI, S.; SHARMA, U.; KRISHNA, R.; SINHA, K.; KUMAR, S. Screening and molecular characterization of cellulase producing actinobacteria from Litchi Orchard. **Current Chemical Biology**, v. 13, n. 1, p. 90-101, 2019. DOI: 10.2174/2212796812666180718114432

LI, S.; SUN, K.; LATIF, A.; SI, Y.; GAO, Y. *et al.* Insights into the Applications of Extracellular Laccase-Aided Humification in Livestock Manure Composting. **Environmental Science & Technology**, 2022. DOI: 10.1021/acs.est.1c08042

LI, Q.; CHEN, X.; JIANG, Y.; JIANG, C. Morphological identification of actinobacteria. **Actinobacteria-basics and Biotechnological Applications**, p. 59-86, 2016. DOI: 10.5772/61461

LIU, K.; MCINROY, J. A.; HU, C. H.; KLOEPPER, J. W. Mixtures of plant-growth-promoting rhizobacteria enhance biological control of multiple plant diseases and plant-growth promotion in the presence of pathogens. **Plant Dis**, 102 (2018), pp. 67-72. DOI: 10.1094/PDIS-04-17-0478-RE

MAMO, J.; ASSEFA, F. The role of microbial aspartic protease enzyme in food and beverage industries. **Journal of Food Quality**, v. 2018, 2018. DOI: 10.1155/2018/7957269

MHIRI, S.; BOUANANE-DARENED, A.; JEMLI, S.; NEIFAR, S.; AMERI, R. *et al.* A thermophilic and thermostable xylanase from *Caldicoprobacter algeriensis*: Recombinant expression, characterization and application in paper biobleaching. **International Journal of Biological Macromolecules**, v. 164, p. 808-817, 2020. DOI: 10.1016/j.ijbiomac.2020.07.162

MSANGOSOKO, K.; BHATTACHARYA, R.; RAMAKRISHNAN, B.; SHARMA, K.; SUBRAMANIAN, S. Cellulolytic activity of gut bacteria isolated from the eri silkworm larvae, *Samia ricini*, (Lepidoptera: Saturniidae). **International Journal of Tropical Insect Science**, v. 41, n. 4, p. 2785-2794, 2021. DOI: 10.1007/s42690-021-00459-x

MOJSOV, K. Microbial alpha-amylases and their industrial applications: a review. **International Journal of Management, IT and Engineering (IJMIE)**, v. 2, n. 10, p. 583-609, 2012.

MOUJEHED, E.; ZARAI, Z.; KHEMIR, H.; MILED, N.; BCHIR, M. S. *et al.* Cleaner degreasing of sheepskins by the *Yarrowia lipolytica* LIP2 lipase as a chemical-free alternative in the leather industry. **Colloids and Surfaces B: Biointerfaces**, v. 211, p. 112292, 2022. DOI: 10.1016/j.colsurfb.2021.112292

MUNK, L.; SITARZ, A. K.; KALYANI, D. C.; MIKKELSEN, J. D.; MEYER, A. S. Can laccases catalyze bond cleavage in lignin?. **Biotechnology advances**, v. 33, n. 1, p. 13-24, 2015. DOI: 10.1016/j.biotechadv.2014.12.008

NALINI, M. S.; PRAKASH, H. S. Actinobacteria: diversity, plant interactions and biotechnology applications. In: **Plant Microbiomes for Sustainable Agriculture**. Springer, Cham, 2020. p. 199-244. DOI: 10.1007/978-3-030-38453-1_7

PHAM, J. V.; YILMA, M. A.; FELIZ, A.; MAJID, M. T.; MAFFETONE, N. *et al.* A review of the microbial production of bioactive natural products and biologics. **Frontiers in Microbiology**, v. 10, p. 1404, 2019. DOI: 10.3389/fmicb.2019.01404

PINHEIRO, V. E.; FERREIRA, J. A.; BETINI, J. H. A.; KAMIMURA, E. S.; POLIZELI, M. L. Utilizing a novel fungal enzymatic cocktail as an eco-friendly alternative for cellulose pulp biobleaching. **BioResources**, v. 16, n. 4, p. 7509-7529, 2021. DOI: 10.1080/14786419.2014.968157

RACHMADONA, N.; HARADA, Y.; AMOAH, J.; QUAYSON, E.; AZNURY, M. *et al.* Integrated bioconversion process for biodiesel production utilizing waste from the palm oil industry. **Journal of Environmental Chemical Engineering**, v. 10, n. 3, p. 107550, 2022. DOI: 10.1016/j.jece.2022.107550

RAHLWES, K. C.; SPARKS, I. L.; MORITA, Y. S. Cell walls and membranes of Actinobacteria. **Bacterial Cell Walls and Membranes**, p. 417-469, 2019. DOI: 10.1007/978-3-030-18768-2_13

RAJKUMAR, J.; DILIPAN, E.; RAMACHANDRAN, M.; PANNEERSELVAM, A.; THAJUDDIN, N. Bioethanol production from seagrass waste, through fermentation process using cellulase enzyme isolated from marine actinobacteria. **Vegetos**, v. 34, n. 3, p. 581-591, 2021. DOI: 10.1007/s42535-021-00239-5

RAMAKODI, M. P.; SANTHOSH, N.; PRAGADEESH, T.; MOHAN, S. V.; BASHA, S. Production of protease enzyme from slaughterhouse effluent: an approach to generate value-added products from waste. **Bioresource Technology Reports**, v. 12, p. 100552, 2020. DOI: 10.1016/j.biteb.2020.100552

RAWLINGS, N. D.; BATEMAN, A. Origins of peptidases. **Biochimie**, v. 166, p. 4-18, 2019. DOI: 10.1016/j.biochi.2019.07.026

RIBEIRO, G. A. L.; MESQUITA, A. F. N.; BANDEIRA, L. L.; CAVALCANTE, F. G.; MARTINS, S. C. S.; MARTINS, C. M. In vitro antagonism of actinobacteria against rhizobia from the soil. **Enciclopédia Biosfera**, v. 19, n. 41, 2022. DOI: 10.18677/EnciBio_2022C15

RODRÍGUEZ-HERNÁNDEZ, D.; MELO, W. G.; MENEGATTI, C.; LOURENZON, V. B.; DO NASCIMENTO, F. S. *et al.* Actinobacteria associated with stingless bees biosynthesize bioactive polyketides against bacterial pathogens. **New Journal of Chemistry**, v. 43, n. 25, p. 10109-10117, 2019. DOI: 10.1039/C9NJ01619H

ROMEU, E.; CAVALCANTE, F.; MARTINS, C.; MARTINS, S. C. Atividade lipolítica in vitro de actinobactérias em gradiente de pH, salinidade e temperatura. **Enciclopédia Biosfera** v. 18, n. 38, 2021. DOI: 10.18677/EnciBio_2021D7

SAHOO, K.; SAHOO, R. K.; GAUR, M.; SUBUDHI, E. Isolation of cellulase genes from thermophiles: a novel approach toward new gene discovery. In: **New and Future Developments in Microbial Biotechnology and Bioengineering**. Elsevier, 2019. p. 151-169. DOI: 10.1016/B978-0-444-63503-7.00009-7

SALWAN, R.; SHARMA, V. Molecular and biotechnological aspects of secondary metabolites in actinobacteria. **Microbiological research**, v. 231, p. 126374, 2020. DOI: 10.1016/j.micres.2019.126374

SALWAN, R.; SHARMA, V. Trends in extracellular serine proteases of bacteria as detergent bioadditive: alternate and environmental friendly tool for detergent industry. **Archives of microbiology**, v. 201, n. 7, p. 863-877, 2019. DOI: 10.1007/s00203-019-01662-8

SARGENT, J. R.; TOCHER, D. R.; BELL, J. G. The lipids. **Fish nutrition**, p. 181-257, 2003. DOI: 10.1016/B978-012319652-1/50005-7

SEGARAN, G.; SUNDAR, R. D. V.; SETTU, S.; SHANKAR, S.; SATHIAVELU, M. A review on endophytic actinomycetes and their applications. **Journal of Chemical and Pharmaceutical Research**, v. 9, n. 10, p. 152-158, 2017.

SENTHIVELAN, T.; KANAGARAJ, J.; PANDA, R. C. Recent trends in fungal laccase for various industrial applications: an eco-friendly approach-a review. **Biotechnology and Bioprocess Engineering**, v. 21, n. 1, p. 19-38, 2016. DOI: 10.1007/s12257-015-0278-7

SHARMA, S.; KUMAWAT, K. C.; KAUR, S. Potential of indigenous ligno-cellulolytic microbial consortium to accelerate degradation of heterogenous crop residues. **Environmental Science and Pollution Research**, p. 1-16, 2022. DOI: 10.1007/s11356-022-21809-3

SHARMA, D.; CHAUDHARY, R.; KAUR, J.; ARYA, S. K. Greener approach for pulp and paper industry by Xylanase and Laccase. **Biocatalysis and Agricultural Biotechnology**, v. 25, p. 101604, 2020. DOI: 10.1016/j.bcab.2020.101604

SIDDHARTH, S. Isolation and characterization of bioactive compounds with antibacterial, antioxidant and enzyme inhibitory activities from marine-derived rare actinobacteria, *Nocardiopsis* sp. SCA21. **Microbial pathogenesis**, v. 137, p. 103775, 2019. DOI: 10.1016/j.micpath.2019.103775

SILVA, V. M.; MENESES, A. C.; MESQUITA, S.; MARTINS, C.; MARTINS, S. C. Atividade pectinolítica de rizóbios de região semiárida. **Enciclopédia Biosfera**, v. 16, n. 29, 2019. DOI: 10.18677/EnciBio_2019A135

SINGH, A. K.; MISHRA, B.; BEDFORD, M. R.; JHA, R. Effects of supplemental xylanase and xylooligosaccharides on production performance and gut health variables of broiler chickens. **Journal of Animal Science and Biotechnology**, v. 12, n. 1, p. 1-15, 2021. DOI: 10.1186/s40104-021-00617-8

SIVAKALA, K. K.; GUTIÉRREZ-GARCÍA, K.; JOSE, P. A.; THINESH, T.; ANANDHAM, R. *et al.* Desert environments facilitate unique evolution of biosynthetic potential in *Streptomyces*. **Molecules**, v. 26, n. 3, p. 588, 2021. DOI: 10.3390/molecules26030588

SOHAIL, M.; BARZKAR, N.; MICHAUD, P.; JAHROMI, S. T.; BABICH, O. *et al.* Cellulolytic and xylanolytic enzymes from yeasts: Properties and industrial applications. **Molecules**, v. 27, n. 12, p. 3783, 2022. DOI: 10.3390/molecules27123783

SUN, K.; LI, S.; SI, Y.; HUANG, Q. Advances in laccase-triggered anabolism for biotechnology applications. **Critical Reviews in Biotechnology**, v. 41, n. 7, p. 969-993, 2021. DOI: 10.1080/07388551.2021.1895053

TRUBITSINA, L. I.; ABDULLATYPOV, A. V.; LARIONOVA, A. P.; TRUBITSIN, I. V.; ALFEROV, S. V. *et al.* Expression of thermophilic two-domain laccase from *Catenuloplanes japonicus* in *Escherichia coli* and its activity against triarylmethane and azo dyes. **PeerJ**, v. 9, p. e11646, 2021. DOI: 10.7717/peerj.11646

VANLEEUEW, E.; WINDERICKX, S.; THEVISSSEN, K.; LAGRAIN, B.; DUSSELIER, M. *et al.* Substrate-specificity of *Candida rugosa* lipase and its industrial application. **ACS Sustainable Chemistry & Engineering**, v. 7, n. 19, p. 15828-15844, 2019. DOI: 10.1021/acssuschemeng.9b03257

VIDMAR, B.; VODOVNIK, M. Microbial keratinases: enzymes with promising biotechnological applications. **Food technology and biotechnology**, v. 56, n. 3, p. 312-328, 2018. DOI: 10.17113/ftb.56.03.18.5658

VIETO, S.; ESCUDERO-LEYVA, E.; AVENDAÑO, R.; RECHNITZER, N.; BARRANTES-MADRIGAL, M. D. *et al.* Biodeterioration and cellulolytic activity by fungi isolated from a nineteenth-century painting at the National Theatre of Costa Rica. **Fungal Biology**, v. 126, n. 2, p. 101-112, 2022. DOI: 10.1016/j.funbio.2021.11.001

VITOLLO, M. Brief review on enzyme activity. **World Journal of Pharmaceutical Research**, v. 9, n. 2, p. 60-76, 2020. DOI: 10.20959/wjpr20202-16660

WALIA, A.; GULERIA, S.; MEHTA, P.; CHAUHAN, A.; PARKASH, J. Microbial xylanases and their industrial application in pulp and paper biobleaching: a review. **3 Biotech**, v. 7, n. 1, p. 1-12, 2017. DOI:10.1007/s13205-016-0584-6.

WANG, Q. D.; LI, S.; ZHANG, K. Y.; ZHANG, Y.; BAI, S. P. *et al.* Protease supplementation attenuates the intestinal health damage caused by low-protein diets in Pekin ducks. **Poultry Science**, v. 99, n. 12, p. 6630-6642, 2020. DOI: 10.1016/j.psj.2020.10.012

WHISTLER, R. L.; DANIEL, J. R. Starch. **Kirk Othmer Encyclopedia of Chemical Technology**, 2000. DOI: 10.1002/0471238961.1920011823080919.a01

ZAKALYUKINA, Y. V.; ZAYTSEV, A. R.; BIRYUKOV, M. V. Study of cellulose-destroying activity of actinobacteria associated with ants. **Moscow University Biological Sciences Bulletin**, v. 76, n. 1, p. 20-27, 2021. DOI: 10.3103/S0096392521010065