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Review

Lipases: Sources of Acquisition, Ways of Production, and Recent Applications

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Abstract

Enzymes are extensively used in biotechnological processes in several areas of industry. They are sustainable and safe, and their specificity is another characteristic that improves the performance in the process. Among enzymes, lipase is relevant due to the ability to play different roles in the industry and the possibility of collecting them from microbial sources that are found in industrial residues. This can reduce the costs of enzyme production. In relation to that, lipase immobilization is an interesting process that allows the enzymes to be reused and improves enzyme robustness. Among them, the cross-linked enzyme aggregates (CLEAs) methodology is attractive due to its simplicity, low cost (given the absence of support), and greater interaction with the substrate. Thus, in this review, we discussed the potential of

lipase. We reviewed the traditional and new sources of obtaining lipases, along with the ways of improving production, activity, and application in the industry.

Keywords
Biocatalyst; Industrial wastes; immobilization; lipase; filamentous fungi

1. Introduction

Enzymes are globular proteins that participate in chemical reactions, making the process faster. They reduce the activation energy, which is essential for the reaction to occur; therefore, enzymes are commonly applied in biotechnological procedures since these molecules have important characteristics, such as specificity and biodegradability, and they can operate in easily controllable environments [1, 2].

In the industrial sector, enzymes are widely used. Besides being sustainable and safe, their application guarantees better performance, providing products with greater functionality and higher yields [3]. Enzymes are used in several fields because of their wide applicability and specificity [4]. The global market of enzymes has been expanding strongly, and in 2019 it was estimated to be $9.9 billion, with a compound annual growth rate of 7.1% from 2020 to 2027 [5].

Hydrolases are a class of enzymes widely applied in the industrial field, with amylases, proteases, and lipases being the most used enzymes [6]. Among the enzymes that are popular in the industrial market, microbial lipases are quite prominent since they have great biotechnological potential and numerous applications, thus attracting higher interest commercially [7].

Lipases are proteins that act in aqueous and non-aqueous systems, in which a phenomenon known as interfacial activation occurs. In the presence of water, lipases catalyze triglyceride hydrolysis to generate molecules of glycerol and fatty acids. However, in media with low water activity, lipases perform reverse reactions, such as esterification and transesterification [8, 9]. The main reactions catalyzed by lipases can be observed in Figure 1, Figure 2 and Figure 3.

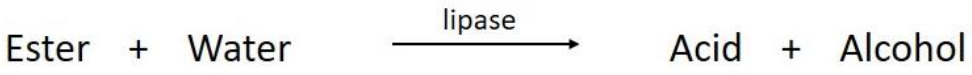

Figure 1 Hydrolysis.

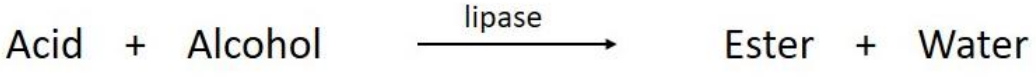

Figure 2 Esterification.

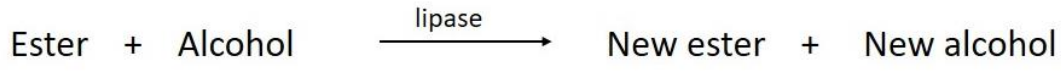

Figure 3 Transesterification.

During metabolic transformations, lipases are extensively used because of their characteristics, such as specificity, availability, no requirement for the use of cofactors, and the ability to operate in large substrate concentrations [10]. Furthermore, they may have regioselectivity and enantioselectivity [11]. Lipases work in open and closed conformations; this mechanism of action of the enzyme is controlled by a kind of lid that hides the catalytic site of the enzyme. A microhydration condition at the active site of the enzyme is necessary for it to move the lid and expose its active site for catalysis [12]. However, in some enzymes, such as the lipase B of *Candida antarctica*, the catalytic site is blocked only partially since its lid is small [13]. Lipase B from *Candida antarctica* adopts a larger opening in aqueous conditions compared to other lipases [14].

Given their robustness, lipases can also be reused, which reduces the cost. The enzymes used need to be recovered for reuse. Recovering enzymes is a very complex process when the enzymes are in their soluble form. To avoid this problem, enzymes might be used in their immobilized form [15].

In this review, we discussed the traditional and alternative sources of lipases, as well as their most recent applications in the pharmaceutical and food industry, among others. The bibliographic review contextualized the most relevant aspects of lipases, providing an overview of the studies that have been conducted, from their production to application. We performed a bibliometric analysis, where the ScienceDirect, PubMed Central, National Library of Medicine, Capes Periodicals, and Google Scholar databases were searched. In this study, we discussed the potential of the lipase enzyme, highlighting its most recent applications, which might serve as a reference for future studies.

2. Traditional Sources

Lipases can be found in several sources and are produced by animals, plants, and microorganisms, including bacteria, fungi, and yeasts. With an increase in the use of this enzyme, it is necessary to discover new sources to supply industrial needs [16]. Industries are particularly interested in lipases of microbial origin which have several favorable characteristics, including resistance to high temperatures, action in a wide pH range, stability in organic solvents, and higher productivity compared to the lipases from other sources [17].

2.1 Plant Lipases

Plant lipases can be found in several types of plants, being present in seeds, grains, fruits, and leaves. However, most lipases are extracted from seeds, especially because they have a greater potential to perform hydrolysis compared to those from the other parts. These sources of lipases have a low production cost and are highly stable in the interesterification processes [18].

The enzymes found in plants have advantages compared to microbial enzymes since their production requires simpler methodologies and does not demand the use of genetic engineering

techniques. These factors reduce the cost of these enzymes by 20 times the cost of the enzymes obtained by fermentation [19]. Plant-derived enzymes are accepted more commonly for application in the food and pharmaceutical areas. However, some disadvantages are associated with the use of lipases, such as the low availability of plants with lipolytic activity in nature, seasonality, and a decrease in the lipolytic capacity, considering the techniques applied for purification [20 apud 18].

Tavares et al. [21] studied the production of lipases obtained from castor seeds and evaluated their hydrolytic potential in cambre oil. The authors observed that the seeds in the natural form showed emulsifying properties, which gives a higher advantage to the hydrolytic reactions. Kouteu et al. [22] investigated the lipase activity on crude extracts of seeds of *Adansonia suarezensis, Adansonia grandidieri, Moringa drouhardii, Moringa oleifera, Jatropha mahafalensis*, and *Jatropha curcas,* and found that all extracts showed ethanolysis and hydrolysis activities.

Lipase was also found in orange residues by Okino-delgado and Fleuri [23]. These enzymes showed good biochemical characteristics, such as action in the broad pH range of 6-9 and optimal temperature around 20 °C to 60 °C, implying high thermostability, and the lipase activity measured was 68.5 lipase U/g. Moreau et al. [24] used sorghum grains as the raw material to extract lipases. The lipolytic activity was estimated by the release of fatty acids. Initially, the levels of free fatty acids were 3.76 ±0.38%, and in the samples stored for 7 and 14 days at 4 °C, the levels were 4.63 ±0.08 and 5.12 ±1.08%, indicating that sorghum grains have lipolytic enzymes.

2.2 Lipases of Animal Origin

Animals are another source of lipases, and the main sources of these enzymes were, initially, the swine and human pancreas. However, their production for commercial purposes currently includes microorganisms as the main source [25], besides other animals, such as sheep, calf, and lamb [3]. To make the use of porcine lipases for industrial application feasible, these enzymes undergo recombinant processes, which allows for even greater yields. Their application in industrial processes is not something usual, given the difficulty in the steps of extraction and purification to obtain the final product [25]. Another reason that prevents the use of pancreatic lipases obtained from animals is that, mostly, these enzymes are impure. Some porcine lipases have amino acids that give a bitter taste, limiting their application in the food industry [26].

The application of animal lipases is more limited to the procedures that involve clinical diagnosis [18]. Despite the low use of these enzymes in the biotechnological processes, the use of porcine lipases is still observed in some activities, such as treating tannery effluents [27] and wastewater from the dairy industry [28].

Sea bass liver lipases were extracted, and subsequently, a crude lipase extract was prepared for use in the degreasing of fish skin, with a lipase activity of 7.24 U/g of tissue. The enzyme exhibited the highest hydrolytic activity for p-NPP at 50 °C and pH 8.0 [29].

2.3 Microbial Lipases

Lipases can be produced by microorganisms, and there is a particular interest of industries in this source of lipase, which is widely used in the field of biotechnology [30]. Microbial lipases are preferred because of several characteristics that make them more attractive when compared to plant and animal lipases. Besides the ease of genetically modifying microorganisms, this source provides high enzyme yields, allowing the production of highly stable lipases [31]. Their capacity to

tolerate organic solvents is one of the factors that make them necessary to conduct biotechnological processes [32, 33]. Microbial lipases are active in a broad range of pH and temperature, and they can also have regioselectivity, chemoselectivity, and enantioselectivity [34].

The reactions catalyzed by lipases represented approximately 20% of the biotransformations performed in 2019, which demonstrates the versatility of this class of enzymes for catalyzing hydrolysis and synthesis reactions [35-38].

Among the lipase-producing microorganisms are fungi, bacteria, and yeasts [39]. Bacterial lipases are resistant to the conditions used in the industry and can be used in several applications, being found intracellularly or extracellularly or attached to the membrane [40]. In the food industry, bacterial lipases are used less often than fungal lipases because of some features, such as lower specificity to the substrate and because they cannot tolerate high temperatures, unlike fungal lipases. Conversely, the production of lipases by bacteria shows higher yields [41]. To obtain bacterial lipases, the most commonly used method is submerged fermentation (SF) [42]. This type of fermentation is especially required for large-scale production since it permits monitoring of the physicochemical parameters necessary for the development of the microorganisms involved [43].

Among the several groups of lipase-producing microorganisms, fungi are the most attractive for industrial application since these sources are frequently extracellular, allowing a simpler extraction [44 apud 60]. Fungal lipases have specific characteristics required by the biotechnological sector, such as stability, specificity, and ease of production [18]. Lipase production by fungi occurs mainly by solid-state fermentation (SSF) processes, which provides an advantage to lipid production since SSF is an extremely economical method [45].

Many microorganisms are good lipase producers. Among them, fungi, especially of the genera *Rhizopus, Aspergillus, Penicillium, Geotrichum, Mucor,* and *Rhizomucor*, yeasts of the genera *Candida, Yarrowia, Pichia, Rhodotorula,* and *Saccharomycopsis*, and bacteria of the genera *Bacillus, Pseudomonas, Burkholderia,* and *Staphylococcus* [4] are notable. Table 1, Table 2, and Table 3 show the lipases obtained from the sources mentioned in Section 2.1.

Table 1 Plant sources for lipase production.

Species	Reference
***Ricinus communis* L.**	[21, 46, 47]
Citrus sinensis	[23]
Oryza sativa	[48]
Cucurbita moschata	[49]
Prunus dulcis	[50]

Table 2 Animal sources for lipase production.

Species	Reference
Sus scrofa domesticus	[25, 27, 28, 51]
Hexaplex trunculus	[52]
Gryllus bimaculatus	[53]
Thunnus orientalis, Totoaba macdonaldi, Morone saxatilis	[54]

Table 3 Microbial sources for lipase production.

Species	Reference
Aspergillus niger	[55, 56]
Serratia marcescens	[57]
Corynebacterium aquaticum	[58]
Bacillus subtilis	[58]
Pleurotus ostreatus	[59]
***Rhizomucor* sp.**	[60]
***Penicillium* sp.**	[61]
Aspergillus flavo-furcatis	[62]
Aspergillus terreus	[63, 64]
Cunninghamella echinulata	[65]
***Geotrichum* spp.**	[66]
Yarrowia lipolytica	[67-69]
Candida antarctica	[34]
Pseudomonas fluorescens	[70]
Burkholderia cepacia	[71, 72]
Staphylococcus warneri	[73]
Bacillus stratosphericus	[74]
Candida rugosa	[75, 76]
Ochrobactrum intermedium	[77]
***Halomonas* sp.**	[78]
Aureobasidium pullulans	[79]
***Pseudomonas* sp.**	[80, 81]
Rhizopus microsporus	[82]
Bacillus amyloliquefaciens	[83]
Pseudomonas cepacia	[84]
Arthrographis curvata	[85]
Rhodosporidium babjevae	[85]
Kluyveromyces marxianus	[86]

2.3.1 Lipases from *Aspergillus niger*

The fungal species *Aspergillus niger* is used in biotechnology for its ability to produce enzymes at high concentrations, as well as for its capacity to produce pharmaceutical supplies that are beneficial to human and animal health [87]. *Aspergillus niger* is an efficient producer of extracellular enzymes, such as amylases, cellulase, and lipases [88]. Notably, *A. niger* lipases are recognized by the FDA (US Food and Drug Administration) as GRAS (generally recognized as safe) substances for use in formulations of products that might be in direct contact with the human body [89].

Several studies have reported on the use of *A. niger* as an efficient lipase producer. Suyanto, Soetarto, and Cahyanto [90] obtained high lipolytic activity (10.83 $U.mL^{-1}$) with *A. niger* by solid-state fermentation using agro-industrial residues as the substrate. Submerged fermentation can also be used in lipase production by *A. niger,* as reported by Lima et al. [55], who evaluated the

effect of the variables on lipase production by *Aspergillus niger C* through submerged fermentation. The kinetics of lipase production in the study showed that high yields can be obtained in a brief period of fermentation which is required in industrial processes, since saving time and energy is important during large-scale production.

One of the main applications of *Aspergillus niger* lipases is biodiesel production [91]. Aliyah et al. [92] used the immobilized enzyme in four cycles for synthesizing biodiesel. Other applications include their use for treating industrial effluents [93, 94]. These lipases might be used in the food industry, considering that they have been used for synthesizing flavor esters [95, 96].

Several studies have been published on lipase production by strains of *Aspergillus niger*. The lipase activity of this fungus depends on the substrate used, as shown in Table 4.

Table 4 The enzymatic activity of *Aspergillus niger* using different substrates.

Substrate	Lipase Activity	Reference
Rice bran	176 U/mL	[97]
Rice bran and glycerol	19.844 U·g	[98]
Soybean meal	163.33 U/g DSS	[99]
Olive oil	5.12 ±0.059 U/mL	[100]
Rice husk, cotton seed cake and red grass husk	28.19 U/gds	[101]
Soybean bran with soy husks	25 U/g	[102]
Rice bran, palm pie, peanut pie and starch	76.7 U/mL	[103]
Mangaba seeds	62.5 U g^{-1}	[104]

2.4 Biochemical Characteristics

The biochemical properties of lipases vary according to the sources, i.e., microorganisms, animals, or plants [105]. Given the great variety of microorganisms with lipolytic capacity, the lipases produced by the different strains present distinct operating characteristics. Some factors can inhibit or stimulate the production of this enzyme. The presence of certain compounds, such as glucose, fructose, and glycerol, leads to the inhibition of lipase production. However, its production is promoted in situations where there are concentrations of free fatty acids, triglycerides, or complex glycans [106].

The cultivation of microbes for enzyme production is affected by several factors. The hydrogen potential (pH) of the fermentation process is an extremely important factor [107]. Some parameters, such as temperature, the composition of the medium, volume of inoculation, aeration, and agitation, can interfere in the process of enzyme production and acquisition [108]. Other conditions that affect lipase production are the nutrients used, such as the carbon and nitrogen sources [30]. In general, lipases act in a pH range between 6.0 and 8.0 and a temperature range of 30-40 °C; however, these values may vary according to the source of the enzyme [109].

Although there is a consensus that these enzymes may act in an optimum pH range of 4-9 and temperature range of 25-70 °C [108], some studies found enzymatic activity at an extremely acidic pH of 2.0 [104], and a highly basic pH of 11.0 [110]. Other studies showed the capacity of lipases to act at high-temperature ranges. For example, Liu, Li, and Yan [111] characterized the lipase of *Pseudomonas fluorescens* and found that the lipase acted at an optimum temperature of 70 °C and remained active at temperatures between 80-100 °C. Colla et al. [45] characterized lipases from

Aspergillus flavus and *Aspergillus niger* by submerged and solid-state fermentation, respectively. The lipases produced by submerged fermentation had 80% stability at an acidic pH, whereas the lipases obtained by solid-state fermentation showed stability higher than 60% at an alkaline pH (Table 5).

Table 5 The biochemical characteristics of some microbial lipases.

Source	Substrate	Optimum pH	Optimum T* (C°)	Inducer	Enzymatic activity	Reference
***Candida* W 3.8**	p-Nitrophenyl Palmitate (pNPP)	7	45 °C	-	2053.3 U/mL	[112]
Aspergillus niger	Rice bran	-	-	Olive oil	282 U/mL	[97]
Yarrowia lipolytica	Mango integument	5	27.9 °C	-	3500 U/L	[113]
Bacillus subtilis	p-Nitrophenyl Palmitate (pNPP)**	8	37 °C	Olive oil	882 U/mg	[114]
Serratia marcescens	p-Nitrophenyl Palmitate (pNPP)	8	50 °C	-	80 U/mL	[115]
Pseudomo-nas helmanti-censis	p-Nitrophenyl Palmitate (pNPP)	7	50 °C	Olive oil	3368 U/mg	[116]
***Sphingobac-terium* sp.**	-	7	37 °C	Olive oil	507.133 U/mg	[117]
Cryptococcus flavescens	-	6	25 °C	Tween 20	0.66 U/mL-min	[118]
Aspergillus niger	Palm pie	-	-	Alkaline palm sludge	72.57 U.gss	[119]
Penicillium citrinum	Soy oil	8	45 °C	Olive oil	271.67 U.g	[120]
Aspergillus terreus	Mustard oil	6	50 °C	Olive oil	942.17 U/mg	[63]
***Halomonas* sp.**	p-nitrophe-nyl laurate	6.9	21.6 °C	-	250 U/L	[78]
Pleurotus ostreatus (Pleo-Lip369)	pNP decanoate	pH 7	30 ±60 °C	-	4000 U/L (*PleoLip241*) 700 U/L *(Pleo-Lip369)*	[59]
Lasiodiplodia theobromae	Coconut residues	6.5	30 °C	Coconut oil	698.1 U/g	[121]
Rhizopus oryzae	Wheat bran	6 (SSF) 5.5	-	Olive oil	62.67 U/mL (SF)	[122]

		(SF)			50 U/mL, (SSF)	
Stenotropho-monas maltophilia	Peanut cake	6	28 °C	-	74,117 U/mL	[123]

T-temperature

The ocean is a favorable environment to obtain enzymes from, as it has a large microbial diversity that favors the acquisition of enzymes with desirable characteristics, such as stability at various pH and temperature ranges and under high pressure and salinity [124]. Lipases from marine microorganisms were recently investigated. Promising sources were found, considering that these microorganisms have activity under extreme conditions [43]. A study performed by Balduyck et al. [125] involved the analysis of two microalgae species, including *Nannochloropsis oculata* and *Tisochrysis lutea*, and the lipases of these marine microorganisms exhibited high activity at 20 °C. Some lipases are active in a wide range of temperatures and pH, as reported by Latip et al. [126], who investigated the properties of lipase of *Pseudomonas* from Antarctica. The lipase produced by the bacterium revealed thermostability at 10-70 °C, and it was also very stable in a broad range of pH, which ranged from 5.0 to 10.0 and showed optimum activity at pH 8.

2.5 Lipase Production: Type of Fermentation and Nutrients

Submerged fermentation (SF) and solid-state fermentation (SSF) are used in enzyme production, in which the substrates involved depend on the type of fermentation. In SF, the substrates are dissolved in a liquid medium, whereas in SSF, solid substrates are used [127]. Lipases have broad specificity to diverse substrates [40, 128, 129]. This capacity to act on different substrates is a key characteristic of lipases, and their enzymatic yield depends on the substrate used. Some of their substrates are triacylglycerides, fatty acid esters, lipids, and synthetic and natural oils [130].

Geoffry and Achur [131] used the effluent from a palm oil factory as the substrate and obtained high lipase activity (7.8 U/mL), thus revealing that the effluent of palm oil factories is a good alternative for the substrate. The lipase produced by *Streptomyces* sp. has good potential in the catalytic processes, although its production is slightly low. Thus, to optimize the conditions of fermentation, Lan, Qu, Yang, and Wang [132] used 4-nitrophenyloctanoate as the substrate and, together with the other optimized parameters, the level of lipase expression increased to 442 U/mL. Salihu, Bala, and Alam [133] showed that peanut pie is a promising substrate for lipase production by *Aspergillus niger*. To reduce the costs of enzyme production, Rodrigues et al. [61] used sesame (*Sesamum indicum)*, sunflower (*Helianthus annus)*, and linseed (*Linum usitatissimum L*.) seed meals as substrates since they have a high lipid value. For all substrates, enzyme production was confirmed; however, the maximum production (160 U) occurred when sunflower seeds were used.

For producing microbial lipases, regardless of the type of fermentation used, carbon and nitrogen sources must be used as nutrients. These nutritional factors directly influence enzyme productivity [30]. During lipase production, the medium must be rich in nutrients. For better enzyme yields, carbon sources, such as glucose, xylose, maltose, lactose, sucrose, glycerol, and other compounds can be added [134]. Numerous oils are described as carbon sources for lipid production; olive oil, palm oil, sunflower oil, and almond oil presented higher enzyme yields in a study by Colla et al. [42]. The synthesis of microbial lipases is controlled by various conditions; however, the carbon source

used in the process is the determining factor for the amount of enzyme produced by the microorganism [135].

In several studies, different carbon sources were tested for lipase production. Jesus et al. [136] evaluated lipase production by *Bacillus subtilis* using manipueira as the carbon source, which is a good alternative source, considering that it can exhibit lipolytic activity in a medium in the absence of inducers. Castiglioni, Costa, and Alegre [137] found a positive effect on the activity of the lipase produced by *Burkholderia cepacia* when the concentrations of soy oil were increased, thus demonstrating that soy oil is a good alternative. Castro et al. [138], in their study, analyzed lipase production by the fungus *Aspergillus westerdijkiae*, and in their experiment, a comparison of enzyme production was performed in a medium supplemented with olive oil as the carbon source and another medium without the addition of olive oil. Their results demonstrated that the yield of lipase activity was around 40,000 U/g in the medium containing 1% olive oil. A reduction in the activity was found when the fungus was cultivated without olive oil, presenting a yield of only 12,000 U/g.

Using appropriate nitrogen sources is crucial to the fermentation process, and the addition of these nutrients directly influences cell growth, as well as enzyme production [139]. The nitrogen sources favor microbial growth, and among the most applied are corn steep liquor, soy flour, yeast extract, peptone, urea, nitrate, and ammonium salts [140]. Many studies used yeast extract as the nitrogen source [55, 85].

Penha et al. [121], in their experiment, concluded that pure palm pie was an incomplete substrate for lipase production by *A. niger* 11T53A14; however, ammonium sulfate solution, as a nitrogen source, was capable of positively influencing lipase production. Salwoom et al. [141] analyzed the nutritional factors involved in lipase production by bacterial strains obtained from the soil of Signy Island. In that study, various carbon (sucrose, maltose, lactose, glucose, and arabinose) and nitrogen (casein, yeast extract, peptone, and tryptone) sources were tested; only the addition of glucose as a carbon source significantly increased enzymatic activity compared to the mean. Other carbon sources reduced lipase production by more than 50%, relative to the nitrogen sources used. A slight increase in lipase production occurred in the presence of peptone, and applying other nitrogen sources slightly decreased the enzymatic activity compared to the mean production.

To achieve a high enzymatic activity, several points must be considered. One of them is the presence of an ideal choice of inducers, a variable that must be investigated by researchers to increase lipase production [142]. In a study, Reinehr et al. [102] tested the production of lipases by *Aspergillus* in the presence of two inducers, i.e., soy oil and glycerol. Their results demonstrated that higher hydrolysis activities were found using 2% soy oil as an inducer, with activity values of 7.69 U/g (*A. fumigatus*), 1.03 U/g (*A. niger*), and 24.17 U/g (*A. niger O-4*). Patel et al. [143] optimized the production of lipase from *Pseudomonas aeruginosa* in their experiments, analyzing several oils as inducers. Among the vegetable oils tested, the best inducer for lipase production was olive oil. A reduction of 15.8% in the activity was found when the inducer was substituted by coconut oil, and the other oils used were classified in the descending order for enzyme production as castor oil > peanut oil > cottonseed oil > sunflower oil. Excessive lipid concentrations in the growth medium might result in cytotoxic effects on the microorganism [144]. Prabaningtyas et al. [99] described the production of a fungal lipase. In their study, enzyme production was evaluated at various inducer concentrations (2%, 4%, and 8% g/g of growth medium), and the highest lipid activity (163.33 U/g of growth medium) was obtained when 4% of the inducer was added to the fermentation process.

Another factor that might interfere in lipase production is the agitation of the growth medium [42]. To optimize the parameters for the production of lipase of *G. thermoleovorans* DA2, Fotouh, Bayoumi, and Hassan [145] adjusted the agitation rate at different rotations per minute, i.e., 40, 80, 120, and 150 rpm. The maximum lipase activity (1,021.91U/mL) was found at 120 rpm, and in the other rotations, the enzymatic activity was lower. Lipase production by *Bacillus cereus* HSS was analyzed by Hassan, Latif, and Ali [146]. The production was evaluated under static conditions and agitation at 120 rpm. They found that the maximum lipase activity was 285 U/mL under the condition of agitation and 225 U/mL in the stationary mode.

2.6 Lipases Produced by Microorganisms Isolated from Industrial Residues

Microorganisms that produce lipase can be found in several types of environments, especially in industrial residues [147]. These industrial effluents are characterized as regions that favor microbial growth and development, as these areas contain high concentrations of free fatty acids that can be assimilated as nutrients and substrates for their metabolism [57]. Peil et al. [148], in their study, isolated microorganisms that could produce lipases in different industrial effluents. The samples were collected in slaughterhouses and dairy industries, and 21 bacteria and seven fungi were isolated. Extracellular lipase production was observed in 71.43% of the bacteria and 57.14% of the fungi.

Lipase production by microorganisms isolated from residues of vegetable oil and petroleum refineries was investigated by Sperb et al. [149]. A total of 24 fungi were isolated and were subjected to qualitative tests for the presence of lipases; only three of them tested positive for lipase activity, including *Aspergillus niger* and two *Rhizopus* species. Padilla, Tabarez, and Orduz [57] collected samples from industrial effluents contaminated with vegetable oils and isolated microorganisms. In that study, the lipolytic enzymatic activity was evaluated under different conditions of temperature and pH. In total, 149 microorganisms were isolated, of which only 37 showed lipolytic activity. For enzyme production, olive oil was used as the substrate, and the optimum pH for the enzymatic activity was 8.0 at 37 °C.

To isolate lipase-producing yeasts, Salgado et al. [150] used wastewater from oil mills as a source of microorganisms. They isolated 32 yeasts, five of which were subjected to tests for determining extracellular lipase activity. Olive oil was used as a supplement in the synthetic liquid medium (YEP). Only JT5 showed a high lipase activity of 0.85 U/mL, and the identification of the strain revealed the yeast *Magnusiomyces capitatus*. The maximum enzyme production by the microorganism mentioned was achieved using the effluent as the substrate, supplemented with yeast extract and olive oil as carbon sources.

Industrial residues from palm oil (palm pie, palm bark, and fiber) were collected for isolating microorganisms with lipolytic activity by Kuncharoen et al. [151], and 16 yeasts were isolated. The strain *Trichosporon insectorum* 4E-1D was the best lipase producer in palm oil and soy oil as carbon sources (28.19 ±4.84 U/mL in palm oil and 22.63 ±0.18 U/mL in soy oil). An industrial effluent rich in organic matter is vinasse, which is a liquid residue from distilleries. It is formed by fermentation, mainly performed in the sugar and alcohol industry [152]. This industrial residue was used by Guan et al. [153], who isolated a new *Lactobacillus* species with lipolytic activity. Three strains were isolated and subjected to lipase activity using olive oil as the substrate. The lipase activities of the three strains varied from 5.88 to 17.79 U/mL. Padma and Vasudevan [154] collected samples from

vegetable market waste tanks to isolate proteolytic and lipolytic microorganisms. The isolate that could produce lipase was a bacterium in the genus *Bacillus*; however, the study did not perform quantitative analysis for determining enzyme production.

Dairy wastewaters are conducive to microbial development, and they were the target of the study conducted by Ficarra et al. (2016) [155], who used these wastewaters as the source of microorganisms to isolate lipase producers. Ogunnusi and Olorunfemi [156] isolated lipolytic bacteria from slaughterhouse effluents and cow manure samples. In total, 12 isolates were obtained, seven of which were from slaughterhouse effluents, and the bacteria were tested for lipase production, with a broth supplemented with oil used as the production medium by submerged fermentation. The bacterium with the highest lipolytic activity was identified as *Pseudomonas aeruginosa* (6.0×10^{-3} mg/mL). The study demonstrated the potential these residues have as sources for enzyme production. Palm oil residues were used for isolating lipase-producing bacteria, and the microorganisms were subjected to fermentation. Hasan et al. [157] evaluated the effect of different carbon and nitrogen sources. Seven bacterial isolates were obtained, and one isolate of the genus *Bacillus* had a maximum yield of 0.168 µg/mL.min using palm oil as a carbon source, whereas, for the nitrogen source, the addition of tryptone to the medium showed the highest enzymatic activity (0.135 µg/mL.min). The optimum pH and temperature for fermentation were 7 and 37 °C, respectively.

Based on these studies, we infer that microbial growth and development occur in different types of environments with distinct characteristics. Among them, industrial residues have been extensively studied as they are a great source of microorganisms (Figure 4). The results, mostly positive, led many authors to search for new lipase-producing microorganisms.

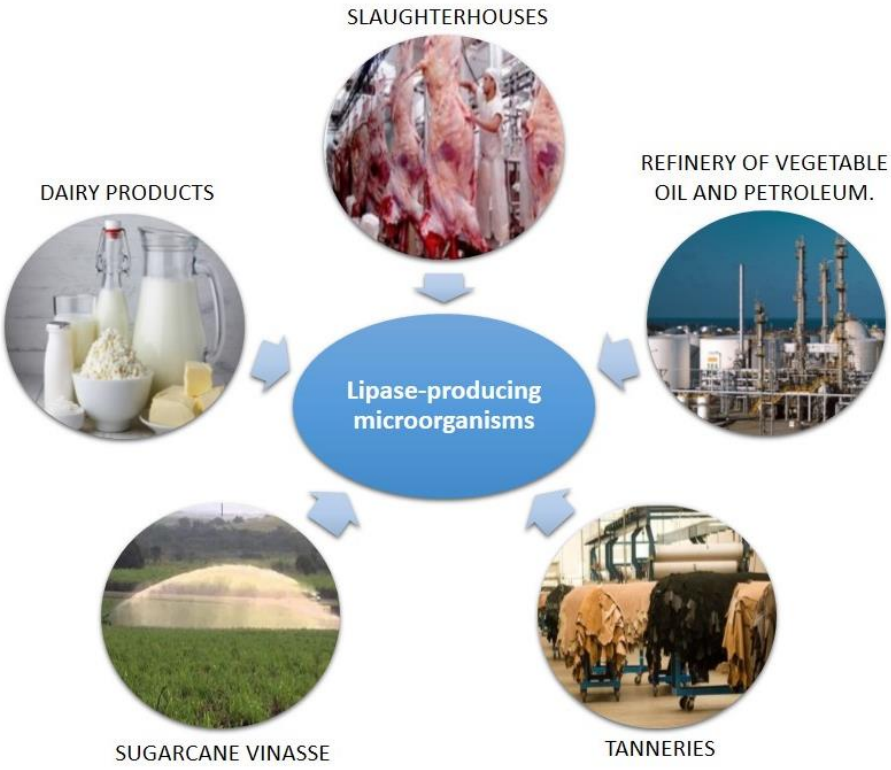

Figure 4 The segments and industries with wastewater rich in organic matter from which lipase-producing microorganisms can be isolated.

2.7 Enzyme Immobilization

The use of enzymes in the industrial field has been impaired by some negative factors associated with these biomolecules. The possibility of denaturation because of their low stability and the complexity in the recovery of the enzyme for consecutive uses make their application challenging in the free form [158]. To solve these adversities, enzyme immobilization techniques aim at facilitating the steps of enzyme separation and recovery since one disadvantage associated with the use of enzymes in the free form is their low stability related to parameters such as temperature and pH [159]. This process of immobilization is based on a bond between the protein and the surface of an insoluble matrix (solid support) [160].

The methods for enzyme immobilization include adsorption, covalent bonding, entrapment/encapsulation, and cross-linking, as demonstrated in Figure 5 [161]. Regarding the immobilization techniques, there is no single methodology that can be used for all enzymes; therefore, for determining the method, some points must be considered, such as the simplicity of the procedure, low cost, and choosing a procedure that provides a satisfactory catalytic activity, besides a technique that allows good operational stability [2].

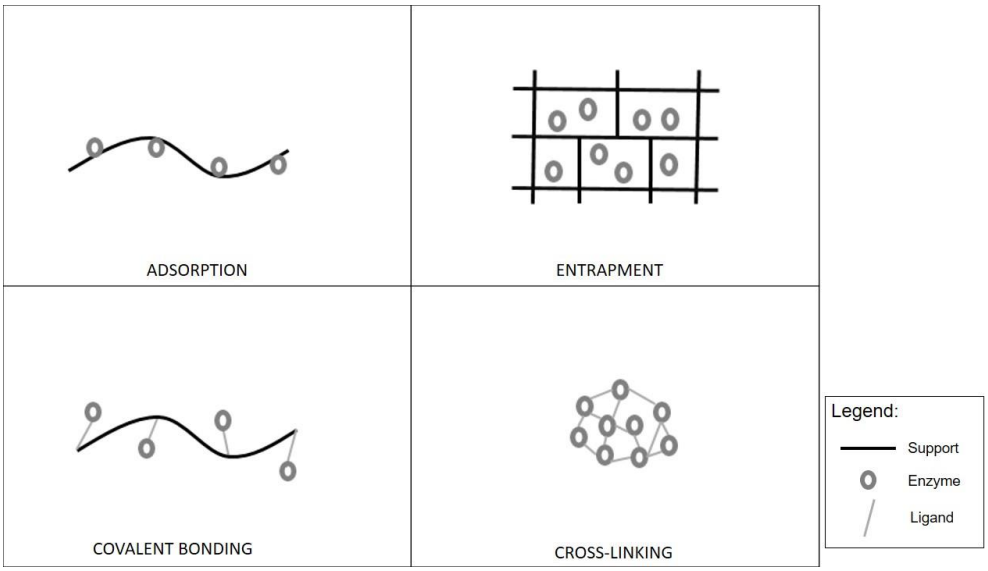

Figure 5 Methods of enzyme immobilization: adsorption, entrapment, covalent bonding, and cross-linking.

An immobilization technique that has attracted attention is known as CLEAs (Cross-Linked Enzyme Aggregates). It is an advantageous method since its methodology is relatively simple and requires a short time to be performed [162]. Proposed by Sheldon [163], CLEAs have interesting characteristics that are desired in industrial biotransformations. The method is very accessible, does not require the use of transporters, two or more enzymes can be co-immobilized, the cost is low, and it allows the retention of high enzymatic activities, as well as has good thermal stability, besides high tolerance to organic solvents. In the literature, there are reports on the use of CLEAs to

immobilize various enzymes, such as lipases [164], cellulases [165], proteases [166], beta-galactosidase [167], amyloglucosidase [168], laccase [169], and acetylesterase [170].

CLEAs are based on two stages. Initially, the enzyme is precipitated by precipitating agents, such as inorganic salts, polymers, and organic solvents, among others. This is followed by the action of cross-linking agents, among which glutaraldehyde is used most commonly as a bifunctional reagent, or by multifunctional agents through reactions with the amino groups present on the surface of the enzyme [171]. Furthermore, this method combines purification and immobilization in a single step, which makes the whole procedure faster and simpler [172].

Dietary proteins might be used alternatively when the enzyme presents a low content of residues of the amino groups on its surface. Thus, to improve the process of cross-linking, the addition of substances that contain many amino groups, such as bovine serum albumin and proteins, is implemented. These substances are called co-feeders [173]. Mafra et al. [174] evaluated the concentration necessary for bovine serum albumin (BSA) (20, 40, and 60 mg) for catalase immobilization in a comparative analysis of enzyme immobilization with and without BSA. It was found that the use of BSA reduces the resistance to mass transfer, and the efficacy factor was 3.7 times greater when bovine serum albumin was used. Two protein feeders were studied by Goetze et al. [175], including feather meal and BSA, for preparing combi-CLEAs to clarify grape juice. Both feeders showed positive effects on the recovery of the activity of the enzyme pectinase; however, the use of feather meal showed higher activity recoveries and was cheaper than using BSA in the immobilization of pectinase.

Several studies have been published regarding lipase immobilization using CLEAs. Picó et al. [176] immobilized lipase B from *Candida antarctica* by the CLEAs method using ammonium sulfate and glutaraldehyde. They found that the reuse of the enzyme was very satisfactory, with biodiesel conversions possible for up to 10 catalytic cycles, retaining 100% of the initial activity. In another study, a lipase from *A. niger* was precipitated using ammonium sulfate, and cross-linking was shown for the first time with the addition of Sodium Tripolyphosphate (TPP). The use of TPP generated favorable results since it provided highly stable enzymes at broader temperature and pH ranges compared to the free enzymes [177]. An advantage of this technique is its ability to make the enzyme more pH stable. JiaoJiao et al. [178] showed that lipase from *Candida rugosa* could be immobilized by the CLEAs methodology and its behavior improved as the enzyme became more stable at a particular pH compared to the free enzyme.

CLEAs and combi-CLEAs are promising immobilization methods, especially because they do not require the use of previously purified enzymes. However, the optimization of the precipitation and cross-linking parameters and the interaction between the parameters is necessary. Their capacity to improve enzyme stability can benefit bioprocesses in industrial applications [179].

2.8 Industrial Applications

The use of microbial enzymes in the industry is an alternative that has been growing considerably, especially because of their use in the food sector, such as in meat processing, dairy industry, beverage production, bakery, and the pharmaceutical industry [180]. Among the industrial enzymes, lipases are prominent due to their versatility, given their exclusive properties [25]. They are widely used in the field of biotechnology, biodiesel production, drug formulation, food industry, and

detergent industry [181]. Other sectors also benefit from the use of lipases, such as the production of cosmetics and the textile and leather industries [182] (Figure 6).

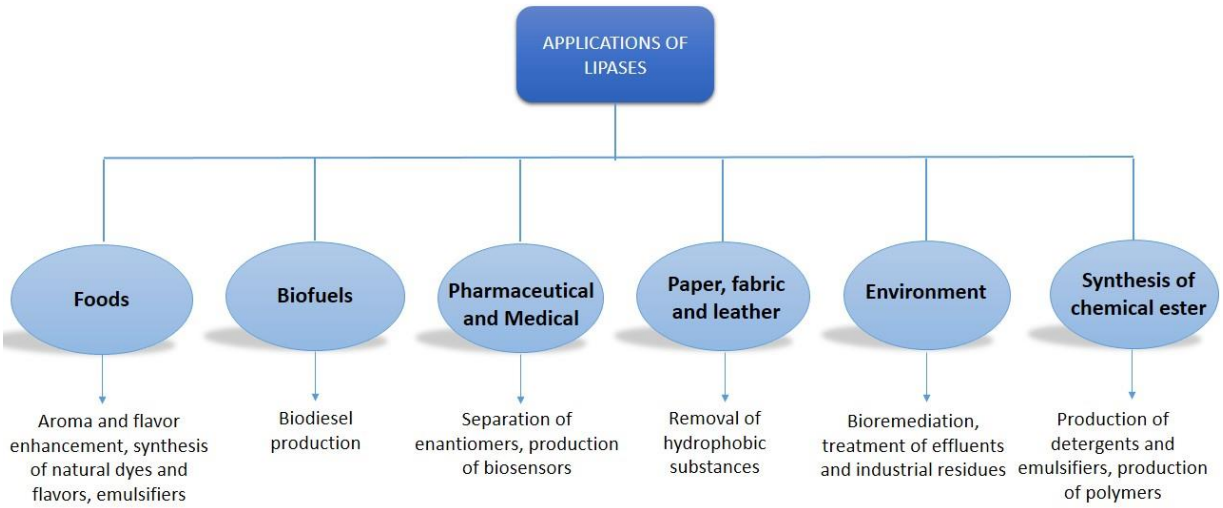

Figure 6 The application of lipase in the industrial sectors. Source: Adapted from Gonçalves Filho, Silva, and Guidini [183].

2.8.1 Lipases in the Food Industry

The food industry uses lipase for various processes, including increasing food quality and yield, providing aromas to certain products, and removing oils and fats. It is used in dairy products, bakeries, breweries, and processing meat, among others [133]. In the dairy industry, lipase hydrolyzes the fat present in milk. Lipase also enhances the flavor of cheese and accelerates its ripening process [184]. Biolipolysis is a process in which lipases are incorporated to remove the fat present in the meat during their processing, to obtain lean meat, and is frequently used in fish meat. Furthermore, microbial lipases are used to refine the flavor of rice, and lipase can also be used in the production of omega-3 [185].

Flavoring substances, such as esters, can be incorporated into the food, cosmetics, and pharmaceutical areas. Natural sources, such as fruits, have these esters. However, their yield is low, and throughout the ripening process of the fruit, their composition is affected. Thus, the use of these enzymes is a feasible alternative for synthesizing these aromatic esters [186]. Lipases are powerful biocatalysts that act in the production of polyunsaturated fatty acids and the synthesis of esters and alcohols. These compounds generated by the action of lipase are used for producing healthy foods and even in the formulation of food supplements [136]. Souza, Ribeiro, and Coelho [187] used a lipase from *Yarrowia lipolytica*, which was obtained by submerged fermentation using soybean meal, to synthesize various flavoring esters with commercial value in the food industry. Free and immobilized lipases were used for catalyzing the enzymatic synthesis of isoamyl acetate and isopentyl acetate esters. Ester conversions were 98.4% and 73.7% for isoamyl acetate and isopentyl acetate, respectively, in a study by Bayramoglu et al. [188]. These results demonstrate the capacity of lipases as potential biocatalysts in the application of aromatic esters.

Another very important function of lipase is its use to expand the shelf life of some shelf products, such as bakery products, and to improve the flavor of juices, soups, sauces, cheeses, and baked

foods. Some properties of noodles improved with the addition of lipase [189]. Cao et al. [190], in their study, found an enhancement in blue cheese by the application of lipase, which influenced the characteristic aroma of the cheese, besides contributing to the typical flavor of the cheese by synthesizing methyl ketones. A study by Schaffarczyk, Ostdal, and Koehler [191] evaluated the influence of the application of lipase in baking. The addition of this enzyme resulted in an increase in the volume of bread from 56% to 58%, depending on the type and concentration of the lipase added. Some lipases can be applied in several sectors, such as the lipase from *Candida rugosa* (CRL), which can help to enhance the aroma and flavor of foods and can be used in the industry of fats and oils, besides being used in other areas [192].

2.8.2 Lipases in Biodiesel Production

Renewable energy sources are now being investigated, especially to substitute the use of the non-renewable ones, which are being depleted rapidly. The production of biodiesel using enzymes received emphasis for being a highly feasible and eco-friendly process, where the degradable oils and fats with a high free fatty acid (FFA) content are used for biodiesel production. These compounds are converted by esterification and transesterification reactions mediated by biocatalysts such as lipases, thus, generating biodiesel as the final product [193].

The lipases from *Burkholderia cepacia*, *Rhizomucor miehei*, and *Candida rugosa* were described by Fan et al. [72] as promising catalysts for biodiesel production, and a comparison of biodiesel production by these three lipases was performed using soybean oil and residual vegetable oil. The results showed that the residual vegetable oil can be effectively converted into biodiesel by the lipase of *R. miehei* through the transesterification process. Luliano et al. [194] used the lipase of *Candida rugosa* to produce biodiesel, using a methodology that involved the conversion of grains used in breweries into biodiesel in the presence of methanol. Good results were obtained with a high yield (98%), and the process also had a low cost since the catalyst could be reused even after four cycles. According to Amini et al. [195], biodiesel can be efficiently produced using the oil of *Ocimum basilicum* seeds as a new source of biodiesel. Immobilized lipase (Novozym 435) and methanol were used for production. The immobilized lipase was reused for up to seven cycles.

Lipases can be used as efficient biocatalysts for producing biodiesel. However, some disadvantages are associated with this practice. For example, the biodiesel generated by this methodology has a low yield, and its use in machines might damage these devices. Additionally, in one of the last production steps, it is difficult to remove the unreacted methanol while producing biodiesel. Thus, additional techniques need to be used to remove the impurities and obtaining high-quality fuel [196].

However, several studies have reported promising results with the use of lipases as catalysts in biodiesel production. For example, in a study by Costa et al. [197], the researchers investigated biodiesel production through the reactions of hydrolysis and esterification. The lipases of *Geotrichum candidum* were used for hydrolyzing soybean oil, and the subsequent step in free fatty acid esterification was mediated by the immobilized lipase from *Pseudomonas fluorescens* (PEL). The hydroesterification mechanism used in the study produced high-quality biodiesel, and the reactions presented favorable viscosity and purity. The hydrolysis reactions presented a complete conversion of the soybean oil within a short period, and the free fatty acids did not require purification, which was advantageous since it reduced the cost. The synthesis of biodiesel by

transesterification, catalyzed by a lipase of *Aspergillus niger*, was studied by Shalini et al. [198]. The immobilized enzyme presented a total biodiesel yield of 90%, and it could be used five times for synthesizing biodiesel with no loss in its activity. Thus, it is an efficient catalyst in biodiesel production. The performance of studies at a laboratory scale, pilot projects, as well as process optimization have advanced the field of catalysts. These studies help to improve enzyme activity and productivity [199].

The use of lipases as biocatalysts has several advantages; however, it is necessary to study the existing methodologies and search for new ways to broaden the use of lipases in the production of this biofuel [200].

2.8.3 Lipases in the Pharmaceutical Industry

In the pharmaceutical sector, the production of pure enantiomers is one of the most significant methodologies since a large percentage of the drugs in progress are chiral. Thus, this production of pure enantiomers is mediated by the action of biocatalysts, especially lipases [201]. This process can also occur by chemical methods; however, the use of enzymatic catalysts is preferable due to their efficiency and selectivity. Additionally, many enantiomers can be produced using these enzymes [202].

Lipases can produce enantiomers. For example, ibuprofen can be produced from certain compounds using a lipase of *Rhodothermus marinus* [203]; atenolol can be produced using a lipase of *Candida rugosa* [204]; milnacipran, a medicine used in fibromyalgia therapy, can be produced using lipases [205]. Other drugs, such as nebacetin, naproxen, ascorbic acid, derivatives of quinolones, ketoprofen, and chloramphenicol, are medicines produced using different types of lipases [206].

The extensive use of these enzymes in the pharmaceutical area derives from their characteristics of regioselectivity and stereospecificity, which are desirable in the biocatalysts used for synthesizing pharmaceutical products [207]. The process of biocatalysis might be visited in the future with a stronger emphasis on the production of medicines and pharmaceutical intermediates [208].

2.8.4 Lipases in the Detergent Industry

Lipases have numerous applications, among which their action in detergent production is emphasized [200]. Lipases break triglyceride molecules into fatty acids, thus generating less emulsion and making it easier to remove triglycerides [209]. In the detergent industry, the aqueous medium is alkaline, and thus, the lipases used in the formulation of detergents must be alkalophilic [210]. The use of enzymes in the formulation of detergents has some advantages, such as a reduction in the time necessary for washing and increasing the life span of the fabric [211].

Studies have shown that microbial lipases can efficiently remove fat. For example, García-Silvera et al. [111] successfully used a lipase of *Serratia marcescens* to remove triacylglycerol of olive oil from cotton fabric. Shrimp hepatopancreas lipases were used in the production of a detergent, and its effectiveness was compared to that of commercial detergents for clothes; positive results were found [212]. A lipase produced by *Bacillus subtilis* showed desirable properties for application in the production of detergents. It was highly resistant to surfactants, oxidizing agents, and commercial detergents and thus could be a strong candidate for use in the cleaning industry [213].

The use of alkaline lipase in the production of detergents can decrease the use of surfactants and other compounds that, from an ecological point of view, are not favorable [214]. Since commercial detergents contain dangerous chemical compounds, both for human and environmental health, lipases represent an alternative for the use of these substances, besides being preferable for their application at room temperature and maintaining fabric quality [40].

2.8.5 Lipases in the Treatment of Effluents

Many industrial residues are released in aquatic environments, which results in the death of aquatic organisms, as these residues contain many oily compounds, which impair the diffusion of oxygen in the water. To solve this environmental problem, enzymes are used to assist in reducing the content of oils and fats present in these residues [215].

Ktata et al. [216] performed the biological treatment of wastewaters using the lipase produced by *Aeribacillus pallidus*. The treatment of the effluents generated by the industry of canned tuna production was highly efficient (96.11%) when lipase was used for hydrolyzing wastewater at 50 °C for 1 h. The lipase of *Bacillus* sp. was evaluated regarding its capacity to hydrolyze fats in different industrial effluents (dairy, bakery, and poultry). The enzyme could hydrolyze more than 50% of the initial fat present in all these effluents, and thus, it was considered to be a good alternative in the pretreatment of these effluents [217]. A reduction of fat by three times was identified in the pretreatment of the effluent from a slaughterhouse when a lipase of *Fusarium verticillioides* was used. The enzymatic activity had an optimum temperature and pH of 45 °C and 5.5, respectively, with the enzyme being stable at a broad pH range (4.0 to 8.0). These properties are desirable for industrial applications [218].

This pretreatment step using lipases is highly feasible since enzymatic hydrolysis allows the subsequent step of the treatment by microbes to be simpler [219]. Studies and new technologies have shown that the enzymes in the pretreatment of industrial effluents reduce the costs involved in this process, besides being eco-friendly [220]. Lipases are often used in the industry; however, their use in the treatment of effluents is limited by their high cost. Thus, the use of these biocatalysts to eliminate the lipids present in the effluents needs further investigation, considering that obtaining high-value by-products in waters with high concentrations of lipids can become attractive and influence the economy [221].

2.8.6 Lipases in Cosmetics

Lipases have been used in the cosmetics industry to produce active compounds or in the catalysis of chemical products, such as esters, aromas, and active agents [222].

In the field of enzymocosmetics, lipases are especially efficient in the formulation of cleaning products and creams for cellulite treatment [223]. Lipases are also used in the preparation of slimming products, as they can break down fat deposits; moreover, hair and makeup products are also created by lipase action. Several products have been synthesized by the catalytic action of lipases, and many of them have been commercialized [222].

A concern of the cosmetic industry is the production of aromas, which are used in fragrances and other products, and this is an important aspect, especially for the consumers. Thus, the industry seeks biotechnological alternatives for the development of natural aromas [224]. Biotechnological processes have been investigated by the cosmetics industry, and the use of biotechnology has led

to the formulation of new products, as well as the optimization of the existing methodologies. The use of enzymes has allowed this sector to provide better products to consumers [225].

2.8.7 Lipases in the Production of Biosensors

Lipases can be used to produce biosensors since their characteristics make them attractive for the manufacture of these materials. Several microbial and animal lipases are used for developing these devices [226]. The advantages of using enzymes for the manufacture of biosensors include high specificity and selectivity, the possibility of regeneration, high yields, and real-time diagnosis. Many biosensors based on enzymatic actions are used in the field of health, such as for domestic monitoring of blood glucose (glucometer) and in portable clinical analyzers [227].

The lipases of *Candida antartica* and *Aspergillus oryzae* were used by Hasanah et al. [228] for developing an optical biosensor to detect triglycerides (TGs). The immobilized lipases can hydrolyze triglycerides, releasing glycerol and free fatty acids. The released acid decreases the pH and the acidity of the medium, which is then detected by an optical pH sensor. Other lipase-based biosensors have been described in some studies. Zehani et al. [229] prepared a conductometric enzymatic biosensor using a lipase of *Candida rugosa* (CRL). This equipment could detect organophosphate pesticides (diazinon, methyl parathion, and methyl paraoxon) in an aqueous medium. In this device, lipase was responsible for catalyzing diazinon hydrolysis. The biosensor presented positive results since it was capable of measuring concentrations as low as 60 µg. Also, for the detection of pesticides, a biosensor was produced with lipases of *Ceratobasidium* sp. by Barboza et al. [230] for carbendazim determination, and in this sensor, the lipase hydrolyzed the substrate p-nitrophenyl acetate (*p*NPA).

The stability of enzymatic biosensors is required in these devices, and their specificity is an important parameter in avoiding false signals. The development of these biosensors is an example of the cooperation between the Biological Sciences and Engineering. Biosensors can be used to monitor health at home, as well as, in hospitals [231].

2.8.8 Lipase in the Textile Industry

Lipases are used in the textile industry, and one of their applications is based on the treatment of fabric. Some conventional treatments use substances that may result in the loss of fabric weight and a higher probability of causing an itch. The substitution of these compounds by lipases reduces the possibility of a reaction, as well as the loss of fabric weight. This enzymatic treatment makes certain fabrics, such as polyester, softer and efficiently modifies the properties of the fabric [232].

Lipases can remove natural oils and fats. Additionally, a high level of dyeing and cleaning performed by this enzyme imparts a high degree of hydrophilicity to cellulosic textiles [233]. Polyester fabrics were treated with lipases by El-Shemy, El-Hawary, and El-Sayed [234]. The enzymatic treatment provided better dyeing capacity, as well as higher wettability and recovery of moisture, and the action of lipase did not promote deterioration of the fabric under the reaction conditions. Taleb et al. [235], in their study, revealed that *Bacillus aryabhattai* can be used to efficiently produce a lipase with a strong ability to remove the lipid barrier from the surface of wool fibers. The enzyme proved to be efficient for bio-cleaning of wool up to five times. The use of the lipase was successful since its application did not deteriorate the fiber properties. Several studies have used lipases for cleaning, restoring, and conserving historic fabrics [236].

The advantage of using enzymes in the treatment of fabric over the conventional methodologies is that the properties of polyethylene terephthalate are maintained since enzymes are large proteins and do not enter the material. Moreover, lipases do not corrode the fabric, an effect that occurs when other substances are used, such as in alkaline treatments [237].

2.8.9 Lipases in Bioremediation

Lipases can be used for the bioremediation of lipid residues [132]. They can clean and decontaminate soil contaminated with greasy residues by converting these contaminants into non-toxic substances [238]. The lipase from *Pseudomonas* sp. was used by Sahoo, Sahu, and Subudhi [239] for the bioremediation of soil contaminated with hydrocarbons from automotive oils. The enzyme used mediated the degradation of this oil, causing 92.6% of the automotive oil to be degraded, thus demonstrating its efficacy in this process.

However, some disadvantages are also associated with the use of enzymes in bioremediation, such as the high cost of enzyme production, the possible inactivation of the enzyme by the conditions used in the process, and limited knowledge of the behavior of the enzymes when they interact with pollutants. Therefore, more studies need to be conducted on the use of enzymes in bioremediation to optimize the parameters and improve the technique [240].

Several industrial sectors use biocatalysis mediated by lipase, and the methodologies used have been studied and optimized. Lipases have been improved due to the association of biotechnology, genetic engineering, and protein engineering, which has allowed the production of several high-quality products. Although there are still some limitations, these inconveniences can be resolved as new technologies are developed [241].

3. Conclusion

Lipases are versatile enzymes used in several industrial sectors, with their activity and biochemical characteristics being greatly influenced by the production source, formulation of the culture medium, and the fermentation method. New microorganisms isolated from residual sources can be an alternative to minimize production costs, besides being the source of new lipases with interesting characteristics required by different industrial segments.

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Author Contributions

Writing and original draft preparation, Myllena R. Santos; Writing and data curation Daniela B. Hirata; Writing-review and supervision Joelise A. F. Angelotti.

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Competing Interests

The authors have declared that no competing interests exist.

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