Fungal Enzymes Involved in Plastics Biodegradation

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Plastic pollution is a growing environmental problem, in part due to the extremely stable and durable nature of this polymer. As recycling does not provide a complete solution, research has been focusing on alternative ways of degrading plastic. Fungi provide a wide array of enzymes specialized in the degradation of recalcitrant substances and are very promising candidates in the field of plastic degradation.

Keywords: plastic ; biodegradation ; enzymes ; fungi ; bioremediation

1. Introduction

The word plastic derives from the Greek “plastikos”, meaning “able to be modeled” [1]. Today, the term plastic refers to a range of synthetic long-chain polymeric molecules which, in the 1950s, started to be substituted for natural materials across a range of different sectors and in everyday applications [2]. The rapid development of plastics can be attributed to their combination of lightness, durability and other intrinsic properties, along with their easy and low-cost production [3]. As a result of their versatility, plastic materials have been increasingly used, reaching global production of almost 370 million tonnes in 2020 [4]. Almost 55 million tonnes of plastic were produced in Europe in 2020 [4]. The most commonly used plastics are polyethylene (PE; 30.3%), polypropylene (PP; 19.7%), polyvinyl chloride (PVC; 9.6%), polyethylene terephthalate (PET; 8.4%), polyurethane (PUR; 7.8%) and polystyrene (PS; 6.1%) [4][5].

1.1. Plastic Pollution

The mass of plastics in municipal solid waste in high-income and developing countries increased from less than 1% in 1960 to more than 10% in 2005 [6]. In Europe, 6.9 million tonnes of plastics were dumped in landfills in 2020 [4]. One of the problems of plastics accumulated in landfills or released into the environment, is the long time they take to decay. This long decay time derives from the inherent characteristics of plastic, especially the high molecular weight, crystallinity and hydrophobicity [3][7], and from the fact that its monomers, such as ethylene and propylene, originate from fossil hydrocarbons [8]. This results in the accumulation and persistence of plastic in land, freshwater, and oceans for many decades [9][10]. Moreover, supplementary chemicals and additives are often added to plastic polymers to increase the quality of the final products [11]. These additives such as endocrine disrupting chemicals (bisphenol A, bisphenol S, octylphenol and nonylphenol) [12], dioxin-like compounds [13] and heavy metals [14][15] can cause negative effects on organisms. Reproductive abnormalities, disruption of the endocrine system, diabetes and obesity could be linked to additives in plastics [16].

A further problem associated with plastic pollution is the formation of small particles called microplastics, which originate from plastic fragmentation. Microplastics and bigger plastic fragments can enter the food chain and be transferred to higher trophic level organisms where they accumulate [17]. Microplastics can also be the carrier for toxic chemicals and pathogens, facilitating their dispersion in the environment and threatening ecosystems [3][5].

In 2020, 12.4 million tonnes of plastics were used for energy recovery [4] and plastic incineration plays an important role in the management of municipal solid waste [18]. However, energy recovery by incineration can lead to harmful and toxic emissions, such as dioxins, furans, heavy metals and sulphides, contributing to environmental pollution [19][20][21]. Recycling is a better alternative for plastic waste management, but it is not the ultimate solution to the plastic problem. For example, the mechanical properties of recycled PET are reduced with each reuse and the thermal degradation of PE by pyrolysis leads to the random breaking of C–C bonds with the consequent drastic change in its mechanical properties [22]. Moreover, the extremely low percentage of PP recycling (<1%) is alarming since in many cases it is not found as the only polymer forming an object. In addition, the tertiary carbon in PP is susceptible to photo-oxidative and thermo-oxidative degradation, requiring a stabiliser to be added in the production stage, contributing to the deterioration of recycled PP properties [22].

1.2. Plastic Biodegradation

Biodegradation is a complex process of physico-chemical transformation of polymers into smaller units mediated by microorganisms [23][24]. Microorganisms, including fungi, are able to biochemically degrade, assimilate and metabolise complex organic compounds, xenobiotics and recalcitrant substances for their energy needs [25][26]. Several organisms and different mechanisms are being investigated at the moment to improve and promote the biodegradation of complex and polluting polymers. For example, the addition of bacteria with specific engineered plasmids in polluted sites could transfer the catabolic genes in the plasmids to the indigenous bacterial population increasing their capacity for xenobiotic degradation [27]. Furthermore, it is possible to insert mutations in bacterial genes that increase the biodegradative capacity of their enzymes. Thanks to this technique, Lu et al. [28] created an algorithm for an engineered and robust PET hydrolase that can be active in a wide range of temperatures and pHs. Another interesting line of research is to exploit extremophile microorganisms, so that they can be used in the bioremediation of extremely polluted sites. For example, some fungi, such as strains belonging to Fusarium, Verticillium, Penicillium and Aspergillus, are able to produce metal nanoparticles that allow them to tolerate and remove heavy metals from heavily polluted water or soil [29].

The first step required for the biodegradation of high molecular weight and long-chain polymers, such as plastics, is the weakening of the polymers' structure. Many different factors can influence plastic biodegradation, for example, the hydrophobicity of the exposed area as well as the chemical structure, crystallinity grade and structure, glass transition, melting temperature and elasticity [30][31][32]. Environmental factors, such as UV exposure or temperature, can decrease the hydrophobicity of plastics or introduce carbonyl/carboxyl/hydroxyl groups, increasing their biodegradability [33][34][35]. These environmental factors can lead to surface roughness, cracks and molecular changes in plastics [36]. Similarly, the growth of microorganisms on plastic surfaces can modify the physical properties of the plastic by creating cracks and enlarging the pore size. Microorganisms can also chemically deteriorate plastics, for example, by changing the pH of the surrounding microenvironment [37].

The second step in plastic biodegradation is the depolymerisation into shorter chains. The microbial exoenzymes involved in this process create intermediates with modified properties, that increase their cellular assimilation [38]. After intermediates are created and assimilated, they are used by cells as carbon sources and broken down into water and carbon dioxide or methane to complete the mineralization process [5][24].

The complexity of plastic biodegradation is due to their chemical and physical characteristics, such as their high molecular weight, hydrophobicity and insolubility [39]. The use of filamentous fungi for the bioremediation process of plastics can overcome this problem. Indeed, filamentous fungi present a typical hyphal apical growth form that allows them to extend their mycelial networks into different kinds of materials [40]. The penetrative abilities of fungal hyphae are associated with their secretion of exoenzymes and hydrophobins, increasing their adhesion to hydrophobic substrates [41]. Moreover, the non-specificity of fungal exoenzymes allows them to break down different plastic polymers [42]. For example, fungal hydrolases (lipases, carboxylesterases, cutinases and proteases) can modify the plastic surface, increasing its hydrophilicity [43]. These enzymes are also involved in PET and PUR biodegradation due to the presence of hydrolysable chemical bonds in the polymer structures [44][45][46]. On the other hand, oxidoreductases (laccases and peroxidases) are involved in plastic degradation into smaller molecules such as oligomers, dimers and monomers [47][48]. Due to their highly stable carbon–carbon (C–C) bonds, plastic polymers such as PE, PS, PP and PVC require oxidation before the depolymerisation process [39][49].

In this context, researchers will examine the different fungal enzymes involved in the degradation processes of the primary petroleum-based plastic polymers, describing their main characteristics, their efficacy and their possible biotechnological applications. Therefore, the aim is to provide an extensive and reliable assessment of all the present knowledge on fungal enzymes in plastic biodegradation as a start base for new bioremediation applications.

2. Fungal Enzymes Involved in Plastic Biodegradation

2.1. Laccases (EC 1.10.3.2)

Laccases (EC 1.10.3.2) are a class of enzyme belonging to the blue copper oxidases and are multicopper monomeric glycoproteins [50]. They use oxygen as an electron acceptor to oxidize phenolic and non-phenolic compounds, and they are involved in the reduction of molecular oxygen to water [51][52][53].

Laccases were first discovered in the plant species Rhus vernicifera in 1883 [54]. In 1896 they were identified in fungi for the first time by Bertrand and Laborde [55][56]. In the following years, laccases were discovered in many species of fungi belonging to Ascomycetes, Basidiomycetes and Deuteromycetes [57]. White-rot fungi are the most studied group in

relation to their ability to produce laccases to degrade lignin [55]. Indeed, in nature, fungal laccases are involved in lignin degradation and in the removal of toxic phenols produced during this process [58]. Moreover, they play a role in the synthesis of dihydroxynaphthalene melanins, compounds that are useful for protection against environmental stress [59]. Thanks to their characteristics, laccases are used in a number of industrial applications such as delignification, pulp bleaching and bioremediation processes removing toxic compounds through oxidative enzymatic coupling [56].

2.2. Peroxidases (EC 1.11.1)

Peroxidases (EC 1.11.1) are a group of haem containing oxidoreductases, which catalyse the oxidation of organic and inorganic compounds and the reduction of hydrogen peroxide [60]. Peroxidases are divided into three classes: class-I are intracellular peroxidases that are found in most living organisms, except animals; class-II are extracellular fungal peroxidases; class-III are extracellular plant peroxidases [61]. The main fungal peroxidases are manganese peroxidases (MnP; EC 1.11.1.13), lignin peroxidases (LiP; EC 1.11.1.14), versatile peroxidases (EC 1.11.1.16) and dye decolorizing peroxidases (EC 1.11.1.19), depending on what they use for the reducing substrate [62].

The most well-known group of peroxidase-producing fungi are the ligninolytic fungi such as white-rot fungi Phanerochaete chrysosporium, Trametes versicolor, Pleurotus spp., Phlebia radiata, Bjerkandera adusta, Ceriporiopsis subvermispora and Dichomitus squalens [60][62][63]. LiP and MnP were first discovered and purified in the extracellular medium of a Phanerochaete chrysosporium culture in the 1980s [64][65][66][67]. Since then, studies have continued to better understand the functioning of these enzymes, and in 2010 the structure of the MnP of P. chrysosporium was refined at 0.93 Å resolution [68].

The main characteristics of peroxidases are their non-specificity and their ability to oxidise substrates with high redox potential [62][69]. These properties have led to these enzymes being used in a large number of applications. Peroxidases are involved in the production of biofuels and paper [70], in waste treatment [60] and in the bioremediation of industrial pollutants such as synthetic dyes and polycyclic aromatic hydrocarbons (PAHs) [40][71][72][73][74][75][76][77].

2.3. Cutinases (E.C. 3.1.1.74)

Cutinases (E.C. 3.1.1.74) are extracellular serine esterases and are divided into two fungal subfamilies and one bacterial subfamily [78]. These subfamilies have a different primary structure according to whether they are eukaryotic or prokaryotic [79]. Cutinases have an α/β fold, and a central β-sheet composed of five parallel strands covered by two or three helices on either side of the sheet [80]. Their active site is uncovered and consists of a catalytic triad of Ser-His-Asp/Glu [81]. One exception is the active site of Trichoderma reesei cutinase, which has a covered active site, similar to a lipase [82]. In this case the imidazole of the histidine removes a proton from the serine hydroxyl group and the serine oxygen makes a nucleophilic attack on the substrate acyl carbonyl carbon [83]. Then, by a transacylation reaction with the serine, the substrate becomes an acyl-enzyme intermediate, which is then hydrolysed to release the product. The development of a negative charge during the formation of the acyl-enzyme intermediate is stabilized by an oxyanion hole of cutinase [80][84].

In nature, because they can degrade ester bonds, cutinases are involved in fungal pathogenesis [80]. Cutinases are also multifunctional enzymes with many industrial applications due to their ability to catalyse hydrolysis reactions, esterifications and transesterifications [85]. These properties make them suitable for the degradation of high molecular weight polyesters [86] and useful in synthetic fibre modification [87].

2.4. Lipases (EC 3.1.1.3)

Fungal lipases (EC 3.1.1.3) are extracellular triacylglycerol acyl hydrolases that can hydrolyse ester bonds from insoluble substrates of tri-, di- and mono-glycerides into free fatty acids and glycerol [88][89]. Therefore, lipases are involved in lipid metabolism in processes such as digestion, absorption and reconstitution [90].

Lipase-producing fungi have been isolated from different habitats such as contaminated soils, wastes and deteriorated food [90][91][92]. . The main genera of lipase-producing fungi are Aspergillus, Acremonium, Alternaria, Beauveria, Candida, Eremothecium, Fusarium, Geotrichum, Humicola, Mucor, Ophiostoma,Penicillium, Rhizomucor, Rhizopus and Trichoderma [88][93].

Fungal lipases are used in a number of industrial applications such as in the food, textile and manufacturing industries and in the production of detergents, cosmetics and pharmaceuticals [94]. Moreover, lipases can degrade fatty wastes [95] and polyurethane (PUR) [96].

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