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Research review paper

From lignocellulose to plastics: Knowledge transfer on the degradation approaches by fungi

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ABSTRACT

In this review, we argue that there is much to be learned by transferring knowledge from research on lignocellulose degradation to that on plastic. Plastic waste accumulates in the environment to hazardous levels, because it is inherently recalcitrant to biological degradation. Plants evolved lignocellulose to be resistant to degradation, but with time, fungi became capable of utilising it for their nutrition. Examples of how fungal strategies to degrade lignocellulose could be insightful for plastic degradation include how fungi overcome the hydrophobicity of lignin (*e.g.* production of hydrophobins) and crystallinity of cellulose (*e.g.* oxidative approaches). In parallel, knowledge of the methods for understanding lignocellulose degradation could be insightful such as advanced microscopy, genomic and post-genomic approaches (*e.g.* gene expression analysis). The known limitations of biological lignocellulose degradation, such as the necessity for physiochemical pretreatments for biofuel production, can be predictive of potential restrictions of biological plastic degradation. Taking lessons from lignocellulose degradation for plastic degradation is also important for biosafety as engineered plastic-degrading fungi could also have increased plant biomass degrading capabilities. Even though plastics are significantly different from lignocellulose because they lack hydrolysable C-C or C-O bonds and therefore have higher recalcitrance, there are apparent similarities, *e.g.* both types of compounds are mixtures of hydrophobic polymers with amorphous and crystalline regions, and both require hydrolases and oxidoreductases for their degradation. Thus, many lessons could be learned from fungal lignocellulose degradation.

Abbreviations: AFM, Atomic force microscopy; BDE, Bond dissociation energy; CAZyme, Carbohydrate-active enzyme; CBM, Carbohydrate binding module; CCR, Carbon catabolite repression; CI, Crystallinity Index; CMF, Chelator-mediated Fenton; EC, Enzyme commission; GMOs, Genetically modified organisms; HDPE, High density polyethylene; HIM, Helium ion microscopy; LDPE, Low density polyethylene; LiP, Lignin peroxidase; LPMO, Lytic polysaccharide monooxygenase; NCDD, Non-catalytic dockerin domains; NMR, Nuclear magnetic resonance; PA, Polyamides (nylon); PBM, Plastic binding module; PBS, Polybutylene succinate; PBSA, Polybutylene succinate adipate; PCL, Polycaprolactone; PDB, Protein Databank; PE, Polyethylene; PET, Polyethylene terephthalate; PGA, Polyglycolic acid; PHB, Polyhydroxybutyrate; PHV, Polyhydroxyvalerate; PLA, Polylactic acid; PP, Polypropylene; PS, Polystyrene; PU(R), Polyurethane; PVAc, Polyvinyl acetate; PVC, Polyvinyl chloride; PVOH, Polyvinyl alcohol; PVP, Polyvinyl polypropylene; SASA, Solvent accessible surface area; SEM, Scanning electron microscopy; VP, Versatile peroxidase.

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1. Introduction

Plastics are a group of materials that include a wide-range of organic-based synthetic and semi-synthetic materials, and have a malleability that allows the materials to be moulded into a variety of shapes. The accumulation of plastic waste is a major societal challenge (Brandon and Criddle, 2019). It is comparable to such recognised ecological risks as greenhouse gas emissions in the atmosphere or land deterioration. By 2050, it is predicted that there will be 12,000 Mt. (million metric tonnes) of plastic waste in landfill sites or the natural environment (Geyer et al., 2017). One visible example of plastic waste pollution is the plastic mulching used in horticulture, mainly non-degradable PE or PVC (Liu et al., 2014a) that are predicted to last in landfills for greater than 300 years before being completely degraded.

Some species of fungi have been found to degrade certain petroleum-based polymers as demonstrated by the following examples: An isolate of *Aspergillus tubingensis* can degrade polyurethane films (Khan et al., 2017). The white-rot *Pleurotus ostreatus* (da Luz et al., 2015) and the ascomycete *Penicillium simplicissimum* can degrade polyethylene (Yamada-Onodera et al., 2001). The brown-rot *Gloeophyllum trabeum* can degrade polystyrene albeit at a low level (Krueger et al., 2017). A recent review summarises how there is much potential amongst fungi for degradation of petroleum-based plastics (Sánchez, 2019). However, in general, the actual degradation by fungi of petroleum-based plastics is low and/or slow, and often occurs for only one or a few types of plastics.

This review proposes a critical cross-assessment of how methodology and knowledge from lignocellulose degradation research could be applied to plastic degradation. A previous review has catalogued microbial degradation of polymers without this critical cross-assessment (Pathak and Navneet, 2017). Lignocellulose is an abundant raw material found in nature and lignocellulose is also massively produced as an agricultural waste product (*e.g.* straw) (FAOSTAT, 2017). In particular, improving the degradation of the lignocellulose-rich materials became a focus of a major societal challenge approximately 15 years ago for cellulosic ethanol production (US-DOE, 2006). This, in turn, led to developments in various methods and technologies. One part of this research focused on understanding how fungi degrade lignocellulose (Mäkelä et al., 2014), including but not limited to examining the whole-organism approach. Moreover, a more thorough and detailed picture was achieved with the input from the molecular and structural analyses of the individual enzymes and proteins involved in lignocellulose degradation. Although a range of microorganisms is involved in both lignocellulose and plastic degradation, this review will focus mainly on fungal degradation (Fig. 1). The purpose of this review is to critically assess how the field of lignocellulose degradation by fungi could influence, impact, and perhaps even inspire the field of plastic waste degradation by these organisms.

2. Overview of biological degradation of plastics

There are various overlapping classifications of plastics, and for this review, their level of biodegradability is considered an important classification (Table 1). Depending on the plastic type, plastic can be produced as either a resin or a fibre or both. There are several major chemical bonds found in plastics, such as C-C bonds (*e.g.,* in the backbone of PE, PP and PVC), amide NH-CO bonds (*e.g.,* in nylon), and ester bonds (*e.g.,* in PET) (Fig. 2). Research on the biodegradability of plastics and the extent of their biodegradability indicate that the presence of hydrolysable ester bonds in plastics such as polyesters contributes to the degradation (Rydz et al., 2014; Vert, 2005). Plastics can also be classified as petroleum-based or bio-based plastics (Gironi and Piemonte, 2011). Bio-based should not be confused with biodegradable. *E.g.,* ethylene produced from sugarcane can be used to make a bio-based PET (Van Uytvanck et al., 2014) that is no-more biodegradable than petroleum-based PET. The vast majority of plastics are manufactured using petroleum-based monomers (Geyer et al., 2017). As also described

Fig. 1. *In situ* degradation of plant material by wood-rotting and cellulolytic fungi. A. Dead wood and plastic waste laying side by side on the forest floor. Dashed and solid line rectangular frames highlight heavily degraded and undisturbed plant and plastic materials, respectively. Nanjing, China. B. *Trichoderma* sp. mould growing on the commercial wood sample.

Table 1
Types and properties of plastics.

Abbreviation	Name	Production type	Biodegradability
PU(R)	Polyurethane	Resin	–
PET	Polyethylene terephthalate	Resin & Fibre	–
PVC	Polyvinyl chloride	Resin	–
PVP	Polyvinyl polypropylene	Resin	–
LDPE	Low density polyethylene	Resin	–
HDPE	High density polyethylene	Resin	–
PS	Polystyrene	Resin	–
PP	Polypropylene	Resin	–
PA	Polyamides (nylon)	Fiber	–
PGA	Polyglycolic acid	Resin	+
PLA	Polylactic acid	Resin	+
PCL	Polycaprolactone	Resin	+
PHB	Polyhydroxybutyrate	Resin	+
PHV	Polyhydroxyvalerate	Resin	+
PVOH	Polyvinyl alcohol	Resin	+
PVAc	Polyvinyl acetate	Resin	+
PBS	Polybutylene succinate	Resin	+
PBSA	Polybutylene succinate adipate	Resin	+

[a]Names of plastics and their biodegradability level were taken from Shah et al. (2008). The relative levels of their biodegradability and whether the plastics are produced as a resin or fibre are indicated. +, represents a biodegradable plastic product; –, represents a plastic product that is not biodegradable.

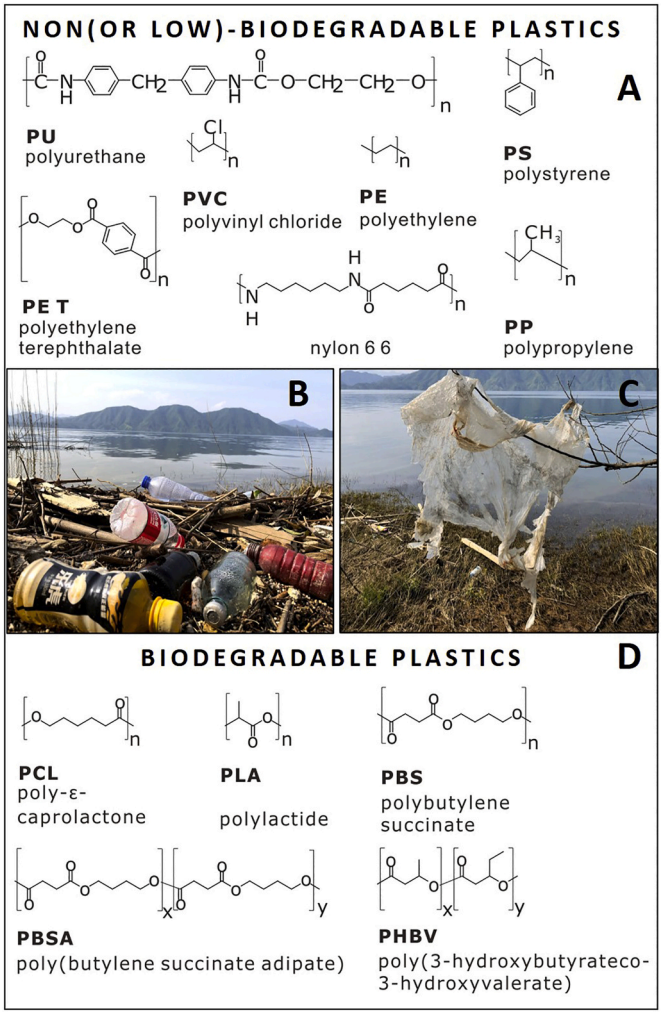

Fig. 2. Chemical structures of the most common petroleum-based plastics. All structures are from Urbanek et al. (2018) except for PU that was taken from Akindoyo et al. (2016).

by Geyer et al. (2017), none of the mass-produced petroleum-based plastics (LDPE, HDPE, PP, PS, PVC, PET, and PUR) can be substantially biodegraded. Still, these polymers do fragment into millimetre to micrometre size pieces that are referred to as "microplastics". These microplastics attract growing concern due to their potential to harm aquatic and terrestrial organisms and enter the food chain (de Sá et al., 2018). This has led to renewed research on plastic degradation to either biodegrade the microplastics or fully biodegrade the mass-produced plastics before they can enter the environment as microplastics. The focus of our review is on how knowledge from fungal lignocellulose degradation can improve the degradation of the mainly non-degradable plastics listed in Table 1, and not the already readily biodegradable plastics.

3. Lignocellulose degradation by fungi

Lignocellulose is composed of polysaccharides (cellulose, hemicelluloses, and pectin) linked with the aromatic polymer lignin, which coats the polysaccharides in order to harden and strengthen the plant cell walls (Marriott et al., 2015; Nishimura et al., 2018). There are various types of lignocellulosic wastes degraded by fungi such as wheat or rice straw, pulp, wood chippings or wood sawdust. Filamentous fungi grow by extending a hyphal network on a surface and secrete enzymes that break down external substrates followed by importing the breakdown products. Native lignocellulose, unless physically injured, is very recalcitrant to microbial and enzymatic attack. Only two groups of basidiomycetes have evolved the ability to degrade wood from dead plants, *i.e.* the so-called "white-rot" and "brown-rot" fungi, which can fully or partially degrade wood, respectively (Floudas et al., 2012; Krah et al., 2018). Ascomycete fungi that can partially degrade wood are referred to as "soft-rot" fungi (Shary et al., 2007). The mechanism of the initial attack on lignocellulose can be primarily oxidative whereby the white-rot fungi attack the lignin by peroxidases or laccases to render the cellulose and hemicellulose accessible. In contrast, the brown-rot fungi use non-enzymatic Fenton chemistry to directly attack the cellulose (Lundell et al., 2010). Once accessible, the polysaccharides are degraded mainly by hydrolytic enzymes (van den Brink and de Vries, 2011). Degradation of cellulose additionally requires enzymes and proteins that aid in the creation of amorphous areas and loosening of the individual cellulose chains (lytic polysaccharide monooxygenases (LPMOs) and swollenins), as well as locating the enzymes at the hydrophobic cellulose surface (carbohydrate binding modules (CBM)) (Kubicek and Kubicek, 2016; Payne et al., 2015).

With regard to the regulation of genes involved in lignocellulose degradation, the expression of genes encoding the polysaccharide-degrading enzymes are induced by sugars (or their metabolic conversion products) released from the polysaccharides (Daly et al., 2016). An extensive understanding of the regulatory system for the genes encoding the polysaccharide-degrading enzymes is mainly known from several model ascomycetes (Benocci et al., 2017). In contrast, there is a poor understanding of the regulatory system for lignin-degrading enzymes whereby the lignin is degraded by oxidoreductases or Fenton chemistry-based approaches (Lundell et al., 2010; Mäkelä et al., 2020). The use of natural-like growth conditions can aid in understanding degradation, such as how the white-rot fungus *Dichomitus squalens* can partially tailor its molecular responses to wood composition (Daly et al., 2018). Fungal degradation can lead to useful intermediates/products, *e.g.,* bioorganic fertilisers (Chen et al., 2011), or can ultimately lead to mineralisation to CO_2. The ability of fungi to secrete high titres of carbohydrate-active enzymes (CAZymes), *e.g.,* hypersecretory mutants of *Trichoderma reesei*, led to the use of fungal enzyme cocktails for industrial saccharification (Peterson and Nevalainen, 2012). Aspects of lignocellulose degradation and their relevance to plastic degradation will be described in more detail in later sections.

In contrast to the polysaccharides in lignocellulose, where monomers are linked together by glycosidic bonds and therefore theoretically

cleavable by hydrolysis, lignin is a complex aromatic biopolymer (Kang et al., 2019) displaying methylester- and C-C bonds. The same bonds occur in many plastics (see the previous section and Fig. 2), although the surrounding bonds can differ. Some of the enzymes acting on lignin could, in theory, be capable of attacking the bonds in plastic polymers.

4. Plastic degradation by fungi

4.1. Fungal enzymes actually or potentially involved in plastic degradation

There is an extensive set of enzyme activities required for the degradation of various plastics and these activities are summarised in Table 2 along with their enzyme commission (EC) number. The activities involved in plastic degradation are mainly hydrolytic, but oxidoreductases are also implicated. As well as the use of EC numbers, other enzyme classification systems such as the CAZy and MEROPS databases, are useful for enzymes involved in plastic degradation. The CAZy database (Lombard et al., 2014) is a resource for carbohydrate-active enzymes and enzymes related to lignin degradation. CAZy families particularly relevant to plastic degradation include AA1 (laccases), AA2 (Class II peroxidases) and CE5 (esterases). Protease/peptidase (EC 3.4.-) activities are annotated in the MEROPS database (Rawlings et al., 2018) and these enzymes can also be applicable to plastic degradation.

Serine proteases purified from commercial preparations, have been shown to hydrolyse various biodegradable plastics such as PLA and PHB (Lim et al., 2005). Nylon, a polyamide plastic with low biodegradability, can be partially hydrolysed by commercial protease cocktails, but the use of proteases here seems focused on textile bio-finishing (Parvinzadeh et al., 2009). As an aside, the polyamide plastics may be more susceptible to the action of certain amidases (EC 3.5.1.4). Recombinant polyamidases from the bacteria *Nocardia farcinica* can hydrolyse polyamide chains in fabrics (Acero et al., 2012; Guo et al., 2013). Proteases from fungi also hydrolyse proteins in plant biomass for at least two purposes: for improving access to the lignocellulose, and for scavenging for nitrogen because in a woody environment, nitrogen is a scarce resource (Cowling and Merrill, 1966).

Ester bond-hydrolysing activities contribute to the degradation of plastics containing ester linkages. A polyesterase isolated from the fungus *Penicillium citrinum* showed activity towards PET and 3PET (Liebminger et al., 2007). Cutinases (EC 3.1.1.74), which are polyester hydrolases, have activity towards PET as reviewed by Nikolaivits et al. (2018). Although as noted by Kawai et al. (2019), care should be taken as to whether cutinases (as well as other activities) are classified as surface modifying or actual PET hydrolases. The activity of a serine hydrolase (a large enzyme class which can include cutinases and proteases) was reported to degrade PUR (Russell et al., 2011). Similar to the protein-degrading enzymes, cutinases are enzymes that are active towards polymers found in plants (cutin is a waxy layer on the surface of leaves) as well as plastics. Cutinases will be described in more detail in later sections on their similarities to cellulases (Section 5.1), and bioprospecting for improved plastic degrading activities (Section 10).

Table 2
Enzyme activities relevant to plastic degradation.

Enzyme activity	Enzyme commission (EC) number
Oxidoreductases	
Laccase	1.10.3.2
Class II Peroxidase	1.11.1.-
Lytic polysaccharide monoxygenase	1.14.99.-
Hydrolases	
Cutinase	3.1.1.74
Amidase	3.5.1.4
Peptidase	3.4.-
Lipase	3.1.1.3

Lipases, another prominent ester-bond hydrolysing activity which catalyse the hydrolysis of lipids, have been shown to be involved in the hydrolysis of various polyesters (Tokiwa and Suzuki, 1977).

Besides hydrolases, lignin-attacking peroxidases can degrade plastics. A manganese peroxidase (MnP) preparation degraded PE, as measured by reductions in elongation and tensile strength (Ehara et al., 2000). An enzyme, purified from a white-rot fungus, considered to be a manganese peroxidase degraded the surface of a nylon-66 membrane (Deguchi et al., 1998). A partially purified lignin peroxidase (LiP) prepared from *Phanerochaete chrysosporium* degraded PVC films (Khatoon et al., 2019). Other enzymes of value, but which have so far not been investigated could be cytochrome P450 monooxygenases (Črešnar and Petrič, 2011), which are important for inactivating xenobiotics by introducing hydroxyl groups at a C-C bond. Cytochrome P450s are abundant in fungi but are mainly involved in the intracellular catabolism of aromatic compounds, but several are also secreted *e.g.,* the fungal pathogen that causes ash dieback has a large number of secreted cytochrome P450s annotated in its genome (McMullan et al., 2018). Finally, glutathione-dependent etherases from white-rot fungi are known to employ the thiolate group of glutathione to attack guaiacyl ethers (Lewis Jr. and Wolfenden, 2019), and could enrich the arsenal of enzymes potentially attacking polyesters.

4.2. In situ fungal plastic degradation

There are various examples of ascomycete and basidiomycete fungi cultured with plastics where degradation of the plastic occurred, with hydrolytic and oxidative mechanisms implicated. A recent review by Sánchez (2019) lists approximately 25 studies where fungal degradation of a petroleum-based plastic was investigated. Other examples of ascomycetes degrading plastic include *Penicillium simplicissimum* which degraded HDPE as shown by gel-permeation chromatography, and also a UV irradiation pretreatment of the HDPE improved the growth of the fungus on the plastic (Yamada-Onodera et al., 2001). Also, *Fusarium solani* was the most dominant species in the fungal community on PU coupons in compost at 25°C while at higher temperatures, the yeast *Candida ethanolica* was the dominant one (Zafar et al., 2013). For wood-rotting basidiomycetes, there are examples of plastic degradation from white- and brown-rot fungi. The lignin-selective white-rot fungus *Phanerochaete chrysosporium* was the first fungus examined to exhibit phenolic resin degradation capability (on a phenol-formaldehyde polymer) (Gusse et al., 2006). The white-rot *P. ostreatus* was shown to degrade oxo-biodegradable plastic bags (d2w) (da Luz et al., 2013), green PE plastic bags (da Luz et al., 2015) and plasma-pretreated LDPE (Gomez-Mendez et al., 2018). Non-enzymatic Fenton chemistry from a brown-rot, *G. trabeum*, was shown to be more effective than a white-rot in PS-sulfonate degradation (Krueger et al., 2015b) but the degradation of the non-sulfonated PS was low (Krueger et al., 2017). The low degradation of the non-sulfonated PS by the *G. trabeum* system highlights the problem in the degradation of low- and non-biodegradable plastics and the challenge that lies ahead. However, it should be stated that fungal degradation can reduce or obviate the need for physical pretreatment (*e.g.* size reduction) of the plastics even though the fungal degradation in itself leads to limited overall degradation of the polymer.

4.3. Mechanistic insights on the degradation of low or non-biodegradable plastics

Recently, there is an increasing amount of research on the degradation of low or non-biodegradable plastics such as polyolefins (*e.g.,* PE or PP). However, the understanding of the mechanisms of the degradation of these polymers is still limited. A recent review on microbial degradation of PS highlights the lack of mechanistic understanding of the degradation of this particular plastic (Hou and Majumder, 2021). Molecular biochemical insights are more developed from bacterial

systems and enzymes than for their fungal counterparts, and thus examples from bacterial systems and enzymes are described in this section. Another recent review highlights some of the challenges of verifying microbial degradation of PE (Montazer et al., 2020). This issue of verifying plastic degradation highlights the importance of caution in searching for mechanistic insights, and here in this section, selected interesting recent examples are described below. Monoxygenases such as alkane hydroxylases have the ability to degrade PE *e.g.* the *Pseudomonas aeruginosa* alkane hydroxylase AlkB can degrade low-molecular-weight PE (Jeon and Kim, 2015). The mechanism for this degradation is assumed to be via terminal hydroxylation as alkane hydroxylases are known to function in this manner (Rojo, 2009). Montazer et al. (2020) noted in their recent review that there were no reports of cleavage of C-C bonds in the backbone of PE due to biodegradation or the appearance of long carbon chain hydrolysis products that would be indicative of the cleavage of C-C bonds in the backbone of PE. This underscores the limited mechanistic understanding of PE biodegradation other than for the low molecular weight PE that the short-chain limited alkane hydroxylases have activity towards.

Another study investigating PE degradation involved an innovative combination of NMR spectroscopy and liquid chromatography-mass spectrometry-based analytical techniques (Eyheraguibel et al., 2017). Here degradation for up to 240 days by the bacterium *Rhodococcus rhodochrous* of oligomers extracted after an oxidative pretreatment of HDPE films was investigated (Eyheraguibel et al., 2017). While intracellular β-oxidation of C-C bonds is considered an important mechanism of chain cleavage, there also appeared to be a substantial contribution from extracellular mechanisms leading to chain cleavages (Eyheraguibel et al., 2017). This was inferred from how longer molecules disappeared more rapidly than their smaller counterparts. Also, as can be expected from a redox perspective, the more oxidized of the oligomeric compounds extracted from the pre-treated HDPE were more efficiently degraded by *R. rhodochrous* (Eyheraguibel et al., 2017).

One interesting and important hypothesis for developing mechanistic understanding of the enzymatic degradation of plastics is the chain-flexibility hypothesis, as described by Inderthal et al. (2021). The chain-flexibility hypothesis relates to how the more flexible the chains in a polymer, the more degradable the polymer becomes *e.g.,* the less crystalline a plastic polymer, the less recalcitrant to degradation. There is support for this hypothesis from how HDPE (containing more closely packed polymer chains) degrades more slowly than LDPE (containing more loosely packed polymer chains) *e.g.,* this trend was observed in bacterial biodegradation of additive-containing HDPE and LDPE films (Fontanella et al., 2010). There is also support for this hypothesis from hydrolysis by a lipase of model polyesters with different chain mobility properties (Marten et al., 2005). As noted by Inderthal et al. (2021), for the plastics that do not have hydrolysable linkages (unlike polyesters such as PET), the degradation appears to be limited to degradation by exo-type mechanisms with little evidence for the existence of endo-type mechanisms. Thus, this limits the ability to test the chain-flexibility hypothesis on these generally non-hydrolyzable plastic types such as the polyolefins, *e.g.*, by using a purified enzyme such as a PETase.

For PET degradation, mechanistic insights into the functioning of PETases are available from bacterial systems. From the *Ideonella sakaiensis* bacterium, a PETase *Is*PETase had its crystal structure reported (Joo et al., 2018). The active site of *Is*PETase appeared to contain sub-sites for the binding of four MHET moieties. Based on structural information, computational molecular docking analysis and biochemical data, the authors proposed a degradation mechanism whereby cleavage can occur at the bond positioned between the two enzyme subsites. Firstly, there is a cleavage internally in the PET backbone at an ester linkage. Then through further cleavage reactions (at the positions between the enzyme subsites) of the two different terminal ends released from cleavage of the PET backbone, terephthalate and ethylene glycol are released (Joo et al., 2018). However, in another study, Wei et al. (2019) were skeptical as they considered the model proposed by Joo et al. (2018) using the oligomeric MHET substrate to be unrepresentative of the stiff PET polymer. Data from NMR indicated the conformation of the PET polymer would be unlikely to interact with the active site of the *Is*PETase in the same manner as the oligomeric substrate, particularly at the reaction temperature of 30 °C that are favourable to the *Is*PETase enzyme (Wei et al., 2019). However, the *Is*PETase degradation model proposed by Joo et al. (2018) may be more representative at higher temperatures, but this would require the engineering of a thermostable *Is*PETase (Seo et al., 2019). These PETase enzymes are related to cutinases, and cutinases will be described in more detail in a later section.

To better understand how research on lignocellulose degradation could provide leads for research on plastic degradation, it is worthwhile considering the similarities and differences between the lignocellulose and plastic polymers and how they are degraded.

5. Similarities between lignocellulose and plastic and their degradation

5.1. Similarities in enzymatic activities required for plastic and lignocellulose degradation

Both hydrolytic and oxidative activities are required to degrade both lignocellulose and plastic polymers. Other sections describe in more detail, the similarities in some of the activities required, *e.g.* protease and peroxidase activities (Section 4.1). This section focuses on the structural (3D structure and conservation of active sites) and enzymatic (pH and temperature optima) similarities between fungal cutinases and fungal endoglucanase I members (as representative of fungal cellulases). Cutinases and cellulases are major enzymes involved in plastic and lignocellulose degradation, respectively.

To date, 3D structural information is only available for five fungal cutinases from *Humicola insolens*, *Fusarium oxysporum* (this species complex has been taxonomically updated to several different species (Maryani et al., 2019)*, F. solani pisi, Glomerella cingulate* and *Aspergillus oryzae* (Table 3). Structurally characterised fungal cutinases share an αβ hydrolase fold and a catalytic triad formed from Ser, His and Asp residues that is typical for serine hydrolases. The overall structure of these fungal cutinases is highly conserved with the enzyme having a globular structure, and the catalytic triad located in a hydrophobic pocket (Fig. 3). A closer look at the sequences by alignment demonstrates the conservation of the residues around the active site (Fig. 4). These cutinases are active on multiple substrates with different chain lengths (mostly from C4 to C16) as well as PET and PCL as indicated in Table 3 (Carniel et al., 2017; Chin et al., 2013; Dimarogona et al., 2015; Kold et al., 2014; Kwon et al., 2019; Liu et al., 2009; Longhi et al., 1997). These fungal cutinases exhibit optimal activity around neutral to alkaline pH. Unlike bacterial cutinases (Nikolaivits et al., 2018), these five fungal cutinases do not have high-temperature activity and do not show a Ca^{2+} dependent thermostability, although Ca^{2+} is used in most of the buffers during enzymatic assays. Total solvent accessible surface area (SASA) was calculated with the VMD Timeline Plugin (Humphrey et al., 1996) for each cutinase structure and this indicated a similar overall SASA for all five cutinases (Table 3).

Likewise, a structural analysis of the catalytic domains of fungal Endoglucanase I (CEL7B) enzymes that belong to GH7 according to CAZy (Lombard et al., 2014) (http://www.cazy.org/), reveals structural similarities (*e.g.* both enzymes have globular structures with highly conserved catalytic residues) and with the obvious differences between cutinases and CEL7B in terms of the substrates they enzymatically degrade. There are a limited number of 3D structures deposited in the Protein Databank (PDB) for fungal Endoglucanase I enzymes. Those shown in Table 4 are from *H. insolens, F. oxysporum* (*Fusarium odoratissimum), Trichoderma reesei* and *Trichoderma harzianum.* All the structures are devoid of the carbohydrate binding modules as attempts for co-crystallisation of catalytic domains with cellulose binding

Table 3
Properties of fungal cutinases with known 3D structures.

Enzyme	Organism	PDB ID	Active site residues[a]	Cofactors	Substrates	Thermal stability	Temperature and pH optima	SASA (A^2)[c]	References
Cutinase (HiC)	*Humicola insolens*	4OYY	Ser105 His173 Asp160	ND[b]	pNP butyrate (C4), pNP octanoate (C8), PET	at 50 °C with over 90% residual activity after 48 h of incubation	50 °C, pH 7 is used in PET degradation experiments	48,183.6	Kold et al. (2014); Carniel et al., 2017); Kazenwadel et al. (2012)
Cutinase (FoCut5a)	*Fusarium oxysporum*	5AJH	Ser121 His189 Asp176	none	pNP acetate (C2), pNP butyrate (C4), pNP laurate (C12), 3PET, BHET, PCL, PET woven fabric with tricot knit	complete deactivation after 2 h at 35 °C, no Ca^{2+} dependent thermostability	40 °C, pH 8.0	49,928.1	Dimarogona et al. (2015)
Cutinase (Cut1)	*Fusarium solani pisi*	1OXM	Ser120 His188 Asp175	ND[b]	Tributyrin (C4), Tricaprylin (C8)	Tm = 56 °C	25 °C, pH 8–8.5, 45 °C, pH 7–10 in the presence of Ca^{2+}	51,601.2	Liu et al. (2009); Longhi et al. (1997); Petersen et al. (2001); Kwon et al. (2009)
Cutinase	*Glomerella cingulata*	3DCN	Ser136 His204 Asp191	ND[b]	pNP caprylate (C8), pNP laurate (C12), pNP myristate (C14), pNP palmitate (C16), PET	lost ~80% of activity after incubation for 1 h at 50 °C	25 °C, pH 8	51,332.6	Nyon et al. (2009); Chin et al. (2013); Seman et al. (2014)
Cutinase	*Aspergillus oryzae*	3GBS	Ser126 His194 Asp181	ND[b]	pNP butyrate (C4), pNP valerate (C5), pNP hexanoate (C6), PCL	Tm = 59 °C	25–40 °C, pH 7.5	51,252.7	Liu et al. (2009)

[a] Active site numbering is based on PDB 3D structure numbering.
[b] Not determined.
[c] Solvent Accessible Surface Area (SASA) calculated with VMD Timeline Plugin (https://www.ks.uiuc.edu/Research/vmd/).

modules are mostly unsuccessful due to the presence of a highly flexible linker domain (Petkun et al., 2015). *H. insolens* CEL7B is not known to possess a CBM at all (MacKenzie et al., 1998; Rasmussen et al., 2020; Schülein, 1997). There is limited data available on the activity and stability of CEL7B from *H. insolens* and *F. oxysporum* (*F. odoratissimum)* (MacKenzie et al., 1998; Sulzenbacher et al., 1996; Sulzenbacher et al., 1997). On the other hand, *T. reesei* CEL7B is a popular choice for mutational and computational studies (Bayram Akcapinar et al., 2011; Bayram Akcapinar et al., 2012; Chokhawala et al., 2015). *T. harzianum* CEL7B has attained attention recently due to its promiscuous activity over a highly acidic pH range and due to its stability (Pellegrini et al., 2015; Sonoda et al., 2019). Structurally characterised fungal Endoglucanase I enzymes share a structurally conserved catalytic domain formed mainly from beta sheets. The open active site cleft harbours the catalytic residues (Glu, Asp, Glu and His residues) as indicated in Fig. 5. CEL7B structures are globular, as indicated by the surface rendering in Fig. 5B, similar to fungal cutinases, and the catalytic residues are also highly conserved (alignment not shown). The loop regions around the active site exhibit changes from the overall structure. The biochemical properties of fungal CEL7Bs are indicated in Table 4, showing how these fungal CEL7Bs are active on multiple cellulosic and synthetic substrates. They exhibit optimum activity around acidic pH and exhibit moderate thermostability similar to fungal cutinases. Total SASA calculated with the VMD Timeline Plugin (Humphrey et al., 1996) for each CEL7B structure indicates similar overall SASA for all four endoglucanases. Perhaps one valuable lesson from lignocellulose degradation for plastic degradation would be to learn from the active site architecture of CEL7B. This may help to design a more effective cutinase active site which might accommodate larger plastic polymers similar to the accommodation of cellulose chains in the CEL7B active site.

5.2. Structural and physico-chemical similarities and their relevance to degradation

There are similarities in the chemical bonds and structures between plant and plastic polymers. Amorphous and crystalline regions are found in plastics (Wei and Zimmermann, 2017) and celluloses (Park et al., 2010). Crystalline polymers tend to be more recalcitrant to degradation compared to amorphous polymers, *e.g.* less crystalline celluloses tend to be more saccharifiable (Cui et al., 2014), and an amorphous PET was modified more than a crystalline PET by a cutinase (Donelli et al., 2010). Two plant cutin monomer units are similar to the plastic polycaprolactone trimer (Pathak and Navneet, 2017). Ester bonds are commonly found in lignocellulose or other plant polymers, *e.g.*, the ester linkages in feruloylated glucuronoarabinoxylan (Dilokpimol et al., 2016) and the ester bonds are also found in polyesters such as PET (Kawai et al., 2019). There is a large variety of both plastic polymers (Table 1) and lignocellulose polymers, *e.g.* hemicelluloses (Scheller and Ulvskov, 2010). Although it may be counterintuitive to describe this diversity of polymer types as a similarity, it means both fields perform their research with a myriad of polymer types in mixed-polymer substrates. *E.g.* although particular activities may differ, both a hydrolytic and oxidative activity may be required for the mixed-polymer substrate and there is a need to temporally and spatially separate these, so the oxidative activity does not inactivate the hydrolytic enzymes (a later section describes the discovery of fungal strategies used to regulate these activities).

With regard to physico-chemical similarities, both lignin and plastics have hydrophobic chemical properties which resulted in both having a water-proofing function (Notley and Norgren, 2010). Overcoming a hydrophobic barrier is critical to enzymatic degradation by hydrolytic enzymes. Apart from the physico-chemical properties of lignocellulose and plastics, physico-chemical pretreatments are often required to improve the accessibility of the lignocellulosic polymers to enzymatic attack (Taherzadeh and Karimi, 2008). Similarly, thermochemical conversions are used for plastic wastes due to the recalcitrance of plastics to

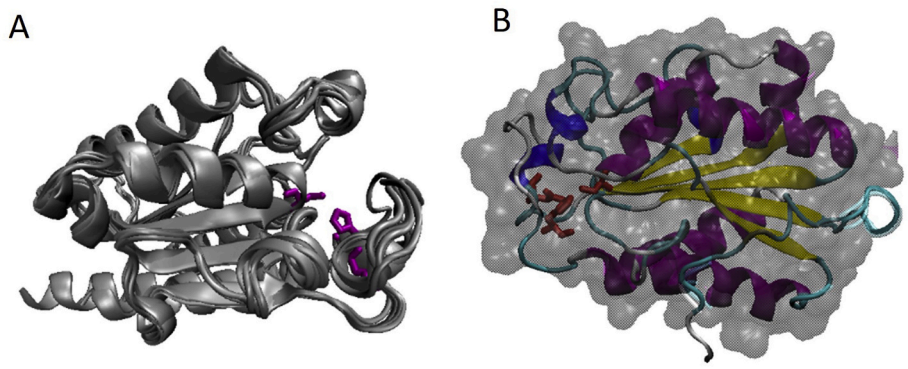

Fig. 3. Superimposed 3D coordinates of the fungal cutinases deposited in the Protein Data Bank (PDB) (www.rcsb.pdb.org). PDB IDs are 4OYY (*Humicola insolens*), 5AJH (*Fusarium oxysporum* f. sp. *raphanin*), 1OXM (*Fusarium vanettenii*), 3DCN (*Colletotrichum gloeosporioides*), and 3GBS (*Aspergillus oryzae*). Superimpositions were performed with VMD using the MultiSeq Plugin (Humphrey et al., 1996). In A) the catalytic triad is shown in purple and in B) in red. In B), the surface area is shown for the 3GBS coordinates in silver. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

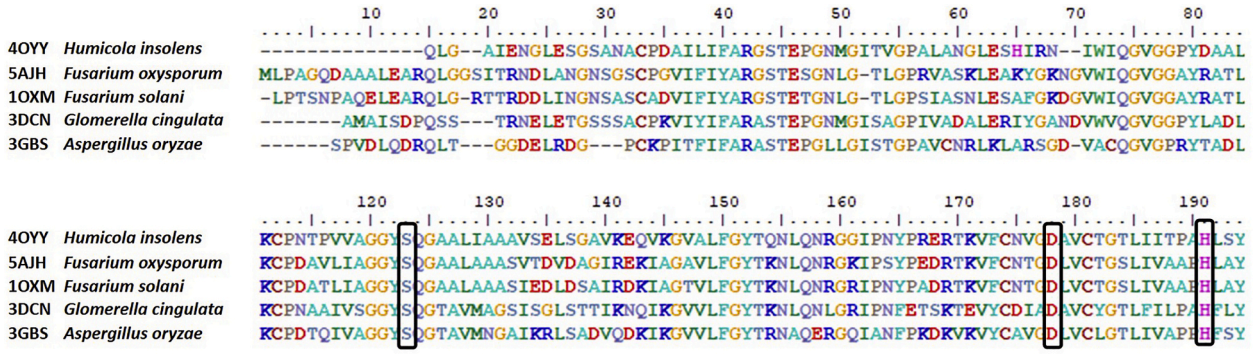

Fig. 4. Multiple amino acid sequence alignment of the five fungal cutinases performed with ClustalW using MEGA7 (Kumar et al., 2016). The catalytic triad is shown with black-outlined boxes.

Table 4
Properties of fungal Endoglucanase I members (CEL7B) with known 3D structures.

Enzyme	Organism	PDB ID	Active site residues[a]	Substrates	Stability	Temperature and pH optima	SASA (A^2)[c]	Reference
Endoglucanase I	*Humicola insolens*	2A39	Glu197 Asp199 Glu202 His213	2,4-dinitrophenyl β-D-cellobioside	structurally stable between pH 5–11 in the presence of SDS	40 °C, pH 5	93,470.7	Rasmussen et al. (2020); Schülein (1997); MacKenzie et al. (1998)
Endoglucanase I	*Fusarium oxysporum*	2OVW	Glu197 Asp199 Glu202 His213	cellobiose	ND[b]	ND[b]	103,754.8	Sulzenbacher et al. (1996); Sulzenbacher et al. (1997)
Endoglucanase I	*Trichoderma reesei*	1EG1	Glu196 Asp198 Glu201 His212	4-methylumbelliferyl β-D-cellobioside, CMC	Tm =65 °C	55 °C, pH 5 (expressed in *P. pastoris*), 60 °C, pH 5	102,809.8	Bayram Akcapinar et al. (2012); Chokhawala et al. (2015)
Endoglucanase I	*Trichoderma harzianum*	5W0A	Glu196 Asp198 Glu201 His212	cellulose, β-glucan, xyloglucan, β-1,4-xylan, arabinoxylan, PASC, pNPC, lichenan, filter paper, Avicel, Sigmacell	Tm = ~58 °C at pH 5	55 °C, pH 3	93,483.3	Pellegrini et al. (2015); Sonoda et al. (2019)

[a] Active site numbering is based on PDB 3D structure numbering, CBMs are absent from the structures. EGI from *H. insolens* is known to lack a CBM.
[b] Not determined.
[c] Solvent Accessible Surface Area (SASA) calculated with VMD Timeline Plugin (https://www.ks.uiuc.edu/Research/vmd/).

enzymatic degradation, such as the production of syngas from plastic-containing municipal solid waste (Drzyzga et al., 2015). Intensive studies about chemical and physico-chemical pretreatments of lignocellulose succeeded in making it susceptible to enzymatic attack. Such intensive studies have so far not been systematically performed with plastic, although it is known that plastics are sensitive to harsh chemical treatments.

6. Differences between lignocellulose and plastics and their degradation

There are fundamental differences between lignocellulose and plastic degradation, especially in comparison with non-biodegradable petroleum-based plastics. While microorganisms have developed strategies to utilise dead plant biomass over billions of years, plastic is known to the environment for only a few decades, a time far too short to enable natural selective pressures to develop degradation strategies for

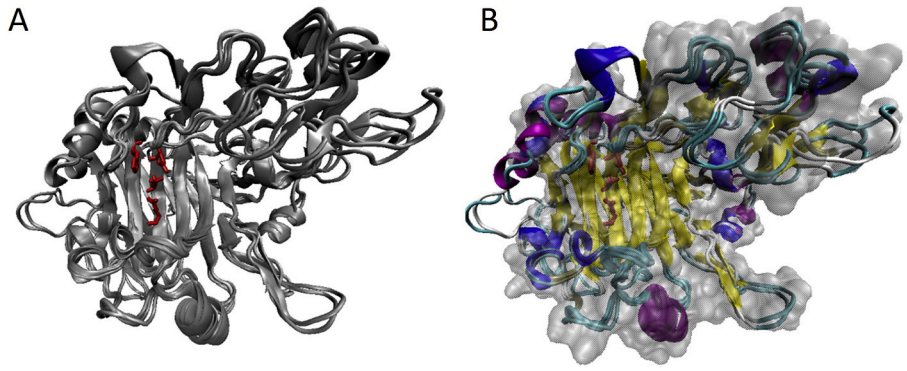

Fig. 5. Superimposed 3D coordinates of sampled fungal Endoglucanase I proteins deposited in the Protein Data Bank (PDB) (www.rcsb.pdb.org). PDB IDs are 1EG1 (*Trichoderma reesei*), 2A39 (*Humicola insolens*), 2OVW (*Fusarium oxysporum*), and 5W0A (*Trichoderma harzianum*). Superimpositions were performed with VMD using the MultiSeq Plugin. In A) and B), the catalytic residues are shown in red for the 1EG1 coordinates (the Endoglucanase I from *Trichoderma reesei*) and in B), the surface is shown in silver for 1EG1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

these chemicals. Furthermore, plastics were designed to withstand environmental degradation by microorganisms resulting in a level of recalcitrance considerably higher than that of lignocellulose.

6.1. Lignocellulose degradation is a natural process

The cellulose and hemicellulose components of lignocellulose in nature can be completely mineralised to CO_2 by microorganisms that possess the required enzymes, whereas lignin is more recalcitrant to degradation, and is often only partially degraded involving modifications that produce humic substances that are essential to soil fertility. Petroleum-based plastics are – for the reason given in the previous section – rarely mineralised to CO_2. Complete mineralisation is an important challenge for plastic degradation, as the partially degraded plastics can accumulate in organisms as toxins (Roy et al., 2011). While the lignocellulose network and cellulose in the secondary cell wall of plants can be highly recalcitrant to degradation, similar polymers can be readily hydrolysed by the plant using the appropriate enzymes, *e.g.* in the primary cell wall, plants evolved to re-cycle the polysaccharides (polysaccharide autodegradation) as well as re-model the polysaccharides as they grow (Barnes and Anderson, 2018). Over millions of years, fungi evolved to degrade plant biomass, *e.g.* one study hypothesised that there was a Paleozoic origin of lignin decomposition (Floudas et al., 2012). The induction of the production of polysaccharide degrading enzymes in fungi is facilitated by sugar inducers (or their metabolic conversion products) released from plant biomass (Benocci et al., 2019; Daly et al., 2016; Liao et al., 2012). To our knowledge, the inducing ability of petroleum-based plastics and their sub-units for the production of enzymes involved in their degradation is unknown.

6.2. Plastic is more recalcitrant to microbial degradation

There is a lack of hydrolysable functional groups in many petroleum-based plastic backbones, which consist of recalcitrant C-C bonds (Fig. 2). There is a higher redox potential required for electron extraction in plastic degradation compared to lignin which is partly due to fewer or a lack of partially oxidised constituents in plastic (oxidised constituents make a more uneven electron distribution and lower the redox potential) (Krueger et al., 2015a). Krueger et al. (2015a) listed bond dissociation energies (BDE) for lignin subunits of 160 and 300 kJ mol^{-1} in case of C–O ether bonds and 240–425 kJ mol^{-1} for C–C bonds. In contrast, for plastics such as PE, PP, PS and PVC, the BDEs are 330–370 kJ mol^{-1} in the C–C bonds of their backbones and 350–470 kJ mol^{-1} for C–H bonds. This presents a challenge for fungal oxidoreductases with the highest redox potential falling short of what is required for plastic degradation. Yet, there are established biochemical reactions that can degrade molecules consisting entirely of C and H (alkanes), and – as part of the physico-chemical challenge to render the molecule susceptible to enzymatic attack – plastics like polyethylene should theoretically be biodegradable. Such approaches should even apply to polypropylene (in which the alkane chain is substituted by a methyl group) and polyvinyl chloride (where it is substituted by Cl-atoms) because the removal of these substituents is theoretically feasible *e.g.* by demethylases or dehalogenases (Ang et al., 2018).

7. Plastics containing or based on components of lignocellulose

Several reviews describe cellulose-based plastic fibres or films (Gilbert, 2017b; Wierckx et al., 2018). Cellulose for processing can be reacted to produce cellulose esters or ethers or instead solubilised and converted back to regenerated cellulose (Gilbert, 2017b). Regenerated cellulose-based plastics were completely degraded in soil after two months (Zhang et al., 1996). Blending various polysaccharides with plastics can increase the degradation rate partly by providing a more degradable carbon source than plastics to support the growth of microbes with plastic-degrading activity. Blending polyolefins (such as PE) with natural polysaccharides (such as starch or chitosan) can accelerate biodegradation (Liu et al., 2014b). There was an interesting suggestion that α-amylases may have promiscuous LDPE degrading activity in an LDPE-starch blend or that a product of the starch breakdown was reacting with the PE (Karimi and Biria, 2019). Here the α-amylases did not have LDPE degrading activity in the absence of the starch but in the presence of the starch, degradation of the LDPE was detected (Karimi and Biria, 2019).

8. Current approaches to improve plastic degradation

The scope of current approaches to improve plastic degradation is limited. Good examples of how advanced uses of fungal lignocellulose degradation research for plastic degradation are few and far between. A less advanced use of lignocellulose research utilised wood chips as a complex inducer of oxidoreductases in the white-rot *Bjerkandera adusta* for subsequent degradation of HDPE (Kang et al., 2019). Generic approaches to improving plastic degradation include screening for plastic-degrading microbes from plastic-contaminated environments, *e.g.* municipal solid waste landfills (Magnin et al., 2019) or plastic debris on a lake shoreline (Brunner et al., 2018). Sulaiman et al. (2012) used a metagenomic approach for the discovery and isolation of a cutinase homolog with PET degradation activity (LC cutinase, LCC) from leaf branch compost.

Cutinases are probably the most advanced example of a plant biomass-degrading enzyme being applied to plastic degradation (Ferrario et al., 2016). An important technique is rational engineering of enzymes to improve their plastic degrading activity. *E.g.* a plastic-degrading aromatic polyesterase from the bacterium *Ideonella sakaiensis* was modified at its active sites by including two conserved residues from cutinases, leading to increased PETase activity (Austin et al., 2018). A LC cutinase with higher amorphous PET degradation activity, was recently engineered to improve its activity and stability (Tournier et al., 2020). A molecular docking and enzyme contact surface-based

analysis was performed with a model substrate to find the site saturation mutagenesis targets around the hydrophobic groove to improve catalytic activity. Most of the variants exhibited lower catalytic activity, whereas the F243I/W variants exhibited improved activity compared to the wild-type LCC. The variants T96M, Y127G, N246D and N246M showed increased stability as indicated by differential scanning fluorometry. Moreover, a disulphide bridge was introduced to the metal (Ca^{2+}) binding sites, thereby creating a D238C/S283C variant to allow thermal stabilisation. This variant showed a 9.8 °C higher Tm (94.5 °C) than the wild-type LC cutinase with a 28% trade-off in catalytic activity (Tournier et al., 2020).

9. Approaches & insights from lignocellulose degradation that have the potential for plastic degradation

9.1. Visualisation of fungal colonisation and degradation of lignocellulose

Microscopic visualisation of fungal degradation of lignocellulose shows how the fungus colonises the surface, the components of the lignocellulose it preferentially degrades, and how differential localised degradation of the lignocellulose occurs.

9.1.1. Techniques and insights for visualising fungal lignocellulose colonisation

The combination of light microscopy and histochemical staining of lignocellulose components has been crucial to understanding wood decay processes as reviewed by Schwarze (2007). Histochemical staining can differentiate particular cell wall components. *E.g.* safranine-astral blue where the safranine stains lignin regardless of the presence of cellulose but astral blue stains cellulose only in the absence of lignin. These histochemical staining techniques visualise where a fungus more readily colonises as well as indicating which cell wall components are being preferentially degraded (Schwarze, 2007). This aided in categorising white-rot fungi as selective lignin degraders or simultaneous degraders of cellulose and lignin.

Conventional histochemical staining has limits on which cell wall components can be reliably identified. More recently, glycan-directed probes (based on antibodies or CBMs) have expanded the identification of specific cell wall components *in situ* (referred to as immunolocalisation) (Pattathil et al., 2015). The antibodies are generated from immunisations using glycans as antigens. Then these antibodies are used to probe the cell wall material followed by detection with a double-labelling immunofluorescence procedure. The CBMs are produced heterologously with a tag such as a His-tag. After probing the cell wall material, the recombinant CBMs are thus detected with a triple-labelling immunofluorescence procedure (Pattathil et al., 2015).

Advances in microscopy have facilitated higher resolution analysis of biological materials, *e.g.* the development of helium ion microscopy (HIM) led to an increase in imaging resolution and depth of field compared to scanning electron microscopy (SEM) (Joens et al., 2013). Using HIM, it was shown how *A. niger* hyphae colonised better on the "rough" compared to on the "smooth" surface of wheat bran (Kowalczyk et al., 2017). Also, HIM visualised the progressive degradation of lignocellulose over time, such as the thinning of cell wall structures in wood colonised by the white-rot *D. squalens* (Daly et al., 2018). SEM has been used to observe friability, fibre separation, and fibrillation of wood cell walls degraded by co-cultures of white- and brown-rot fungi (Giles et al., 2015).

Fungi grow as a mycelial network (Fricker et al., 2017) and visualisation of this network is crucial to understanding the colony dynamics and network architecture when fungi grow, *e.g.* network analysis of cord-forming fungi such as *Phanerochaete velutina* (Wood et al., 2006). The methods developed and applied here are also important for temporal and spatial understanding of the colony dynamics during plastic degradation.

9.1.2. The visualisation of plastic degradation lags behind that of lignocellulose degradation

From research with fungi and plastic degradation, it is more common to analyse the degraded plastic microscopically after the fungus has been removed, *e.g.* Khan et al. (2017), rather than a real-time analysis of the plastic while it is being degraded by a fungus. There is a lack of histochemical staining-type methods as well as glycan-directed type probes for plastics. Plastic-directed probes that are analogous to CBMs may be less complicated to develop compared to antibody-based probes or histochemical stains. There are already CBMs that can bind to PET (Weber et al., 2019) and polyhydroxyalkanoate (a microbe produced biodegradable polyester-based plastic) binding modules are an example of a plastic binding module (PBM) (Ribitsch et al., 2013). Development of these techniques that could identify plastic substructures could then aid in categorising how different fungi degrade plastics (*e.g.* the plastic equivalent of the white-rot, brown-rot and soft-rot classification). A starting point could be the use of histochemical staining or glycan directed probes against the polysaccharide components of plastic-polysaccharide blends, *e.g.* for the starch component of plastic-starch blends with monoclonal antibodies raised against starch ((Rydahl et al., 2017)). A challenge for visualising plastic degradation by fungi is the potential requirement to develop standardised co-substrates that function as a carbon source to support growth. This is especially challenging for the non-biodegradable petroleum-based plastics which generally cannot function (at least not initially) as a carbon source.

9.2. Decay mechanisms and strategies

The decay strategies used by fungi can be insightful for improving plastic degradation. Different fungal wood decay strategies can be classified as white-rot, brown-rot, or soft-rot, depending on how the wood components are decayed (Hildén and Mäkelä, 2018). Research on improving saccharification of lignocellulose to make biofuels has benefited from research on understanding aspects of these decay strategies. Part of this is a type of (bio)mimicry whereby a replication of what happens in nature is attempted for an industrial application. The biomimicking of the chelator-mediated Fenton (CMF) system for the pretreatment of spruce wood is a good example. However, the approach has met with limited success (Hegnar et al., 2019).

9.2.1. How to orchestrate hydrolytic and oxidative mechanisms?

Both hydrolytic and oxidising activities or non-enzymatic oxidising mechanisms are required for the degradation of wood. Hydrolytic activities are primarily used for degradation of polysaccharides and oxidoreductases or non-enzymatic mechanisms, such as the CMF system primarily for the degradation of lignocellulose. However, the polysaccharide-degrading hydrolytic enzymes can be inactivated in the oxidising environment required to degrade the lignin. The same problem is present in the biological degradation of plastics, where both hydrolytic (*e.g.* cutinases) and oxidative (*e.g.* laccases) activities are required.

Recent research with brown-rot fungi discovered key aspects of how to orchestrate hydrolytic and oxidative mechanisms. The brown-rot *Postia placenta* uses a staggered decay mechanism to spatially separate the gene expression related to the oxidative mechanism from the expression of the genes encoding hydrolytic activities (Zhang et al., 2016). Further subsequent work elaborated on the mechanisms with the identification of avoidance, quenching and tolerance mechanisms (Castaño et al., 2018). Avoidance involved producing the oxidising environment primarily at earlier stages of decay where the conditions were more conducive to the generation of hydroxyl radicals. Quenching involved producing antioxidants, possibly fungal phenolic compounds, to reduce the oxidising level of the environment. As part of the tolerance mechanism, there was evidence that *P. placenta* CAZymes were more redox tolerant than their *T. reesei* orthologs (Castaño et al., 2018). Also, the *P. placenta* enzymes secreted earlier (when the conditions were more oxidising) were more tolerant of oxidising conditions than the enzymes

secreted later.

Brown-rot fungi have been shown to degrade PS-sulfonate using what was considered a Fenton chemistry-based approach (Krueger et al., 2015b). The degradation of the non-sulfonated PE was lower (Krueger et al., 2017). Still, perhaps the degradation rate can be increased with the insights from the above mechanisms which could develop more optimal culturing techniques that take into account how a brown-rot fungus is attempting to orchestrate hydrolytic and oxidative degradation mechanisms.

9.2.2. Paleogenetics and understanding the evolution of decay strategies

Paleogenetics is the resurrection of ancestral enzymes of now-extinct organisms by phylogenetic prediction followed by heterologous enzyme production (Garcia and Kaçar, 2019). Paleogenetics can be informative for understanding the evolution of a particular activity. A challenge in the use of redox enzymes such as laccases and Class II heme peroxidases in the degradation of plastics is that the redox potential is insufficient compared to what is required to oxidise lignin. It can be insightful for plastic degradation to understand how extant lignin peroxidases achieved sufficient redox potential for lignin degradation, albeit still insufficient for what is required for plastic degradation (Krueger et al., 2015a).

White-rot fungal decay strategies appear to have evolved higher redox potential enzymes to degrade lignin (Ayuso-Fernández et al., 2018). A paleogenetics approach traced the emergence of lignin peroxidases. These enzymes have a flat-surface exposed tryptophanyl radical that can directly oxidise the lignin polymer (Ayuso-Fernández et al., 2018). The paleogenetic analysis suggested that the lignin peroxidases with higher redox potential evolved concurrently with lignin that required higher redox potential for its degradation (Ayuso-Fernández et al., 2019). How these lignin peroxidases evolved their higher redox potential ability could inform further engineering of peroxidases for even still higher redox potential that could degrade plastic. One intriguing hypothesis is that perhaps in an earlier geological age, there was a requirement for enzyme activities that co-incidentally are also better at degrading man-made plastics than those enzymes found in extant organisms. Underlying the paleogenetics approach is a requirement for extensive genomics connected with phenotypic information of extant species to aid inferences about the ancestral proteins.

9.2.3. Carbohydrate binding modules (CBMs)

CBMs are protein-domains that can bind to carbohydrate structures and they are generally attached to a catalytic domain with the overall aim of directing the catalytic domain towards its target substrate (Boraston et al., 2004). One bacterial CBM in particular out of a set of eight (including two from fungi) from diverse CBM families that were screened for binding to PET films exhibited strong binding to the plastic (Weber et al., 2019). Polyhydroxyalkanoate binding modules are an example of a plastic binding module (PBM) although PHA is a biodegradable microbially synthesised rather than man-made petroleum-based plastic (Ribitsch et al., 2013).

9.3. Overcoming hydrophobicity of lignin

9.3.1. Hydrophobicity and how it is measured

Hydrophobicity is the physical property of a molecule that results in little or no attraction to water molecules. The hydrophobic physical property of both plastics and lignin results in them having a water-proofing function (Notley and Norgren, 2010). Plants evolved to use lignin in the walls of xylem vessels, and these vessels are used to transport water. Hydrophobic surfaces, which repel water as well as repelling other hydrophilic molecules, can be a problem for enzyme function because the external surface of an enzyme is usually hydrophilic (*e.g.* the hydration shell of an enzyme). Also, enzymes generally require water for proper functioning (Rezaei et al., 2007) and in the case of hydrolytic enzymes, these also require water for their enzymatic reaction.

The contact angle of a drop of liquid on a surface indicates how hydrophobic or hydrophilic the surface is. The larger the contact angle, the less wettable (more hydrophobic) the surface is. The contact angle measurement of various plastics is listed by Chiou and Hsieh (2015). Lignin might not be strictly considered hydrophobic as the contact angle can be <90 °C (Notley and Norgren, 2010), but is widely regarded as having hydrophobic properties.

9.3.2. Amphipathic molecules such as hydrophobins and degradation of hydrophobic surfaces

Hydrophobins are low molecular weight, secreted amphipathic molecules which contain both hydrophobic and hydrophilic patches. There is support for a role of hydrophobins in lignocellulose degradation. Hydrophobins were co-expressed with plant biomass-degrading CAZymes in *A. niger* cultured with wheat straw or willow (Delmas et al., 2012; Pullan et al., 2014). In *A. nidulans*, deletion of the gene encoding the hydrophobin RodA resulted in reduced retention of CAZymes in the vicinity of the fungal biofilm on steam-exploded sugar cane bagasse (Brown et al., 2016). The role of hydrophobins is not limited to lignocellulose degradation, as these amphipathic proteins have a wide range of functions, such as allowing hyphae to breach the air-medium interface and making spores hydrophobic to facilitate their dispersal through the air.

Hydrophobins can be classified as either class I or class II based on their solubility in water. Class I hydrophobins are usually considered as insoluble and this limits their usefulness for plastic degradation, while class II can be found in the culture medium. Hydrophobins are only found in filamentous fungi and are one of the major reasons for specifically analysing aspects of fungal (as opposed to bacterial) degradation of plant biomass for improving plastic degradation. Hydrophobins have a wide and growing range of applications (Berger and Sallada, 2019). There are several examples of how hydrophobins can improve the enzymatic degradation of certain plastics. The *A. oryzae* hydrophobin RolA recruited a polyesterase CutL1 to the surface of PBSA to improve degradation of this biodegradable polyester (Takahashi et al., 2005). A later study showed that the RolA-CutL1 interaction was mediated by ionic interactions (Takahashi et al., 2015). The fusion of a *Trichoderma* hydrophobin to a bacterial cutinase improved hydrolysis of PET up to 16-fold over the level of the free enzyme (Ribitsch et al., 2015). The diversity of hydrophobins is likely greater than what is known and thus the need for further genomics and structural studies to understand more of the diversity. Studying diversity is relevant to applications as it has been shown that the stimulating effect on cutinase activity can depend on the particular hydrophobin used (Espino-Rammer et al., 2013). Genomics approaches are discussed in more detail in a later section.

9.3.3. Sensing of a hydrophobic (or solid) surface

There are known signalling cascades or other molecular mechanisms about how particular models or plant pathogenic fungi interact with the plant surface (Zeilinger et al., 2016) or a range of different solid or semi-solid surfaces (Kumamoto, 2008). It is unknown whether or to what extent these mechanisms are activated or functioning when fungi make contact with plastic surfaces. The role of cutin as a source of signals is reviewed by Serrano et al. (2014) where components of the cuticle can be perceived by invading plant pathogenic fungi and can activate developmental processes in the fungi. Whether the polycaprolactone trimer (which is similar to the cutin dimer) can signal similarly would be of interest to fungal sensing of plastic surfaces. Already, most of the screening of fungi for cutinase activity is performed in minimal medium containing PCL or cutin. It would be relatively straightforward to use this enzymatic screening approach for a comparative transcriptomic or kinase-activity study to investigate similarities in the functioning of the sensing pathways on PCL and cutin.

9.4. Fungal degradation of crystalline cellulose

Insights from how fungi degrade crystalline cellulose can aid in understanding how fungi can degrade plastics. Cellulose and plastics can both have crystalline and amorphous regions, and the level of crystallinity can vary from one plastic polymer to another (see Table 1). Crystallinity has structural benefits for both cellulose and plastics as it makes the structure more rigid so it can support a greater load, but it is then a barrier to enzymatic degradation as the inside of the crystalline structure is inaccessible to enzymes. Therefore, the rate-limiting step in the bioconversion of cellulose from plant biomass into biofuels is the hydrolysis of cellulose, especially the crystalline regions. Cellulose is more digestible with lower crystalline content and higher amorphous content (Cui et al., 2014). For example, pretreatment of wheat straw with ionic liquids lowers crystallinity and improves saccharification by a commercial enzyme cocktail as well as when cultured with *A. niger* (Daly et al., 2017a). In nature, fungi have evolved ways to overcome this crystallinity barrier through the secretion of different cellulase components which can preferentially act on either crystalline or amorphous cellulose. For example, *T. reesei* cellobiohydrolase I (CBHI) was shown to hydrolyse crystalline cellulose from hydrophobic faces. Real-time imaging of the single enzyme molecules through atomic force microscopy (AFM) showed that they were only able to bind to *Valonia* cellulose crystals from the hydrophobic face (Liu et al., 2011). Additionally, it has long been known that a 50 A° long tunnel-shaped active site architecture allows this specific exoglucanase enzyme to processively hydrolyse cellulose chains in the highly ordered crystalline regions from the reducing ends towards the non-reducing ends (Yeoman et al., 2010). Both white- and brown-rot fungi (in lignocellulosic substrates) have exhibited rapid depolymerisation capability of both amorphous and semi-crystalline cellulose resulting in varied length cellulose chains and increased microfibril permeability (Giles et al., 2014; Kleman-Leyer et al., 1992).

9.4.1. Crystalline materials and how crystallinity is measured

A crystalline material consists of a layered lattice structure held together predominantly by ionic bonding. There are various methods, such as X-ray diffraction and nuclear magnetic resonance (NMR) used to measure crystallinity (Gilbert, 2017a). Crystallinity Index (CI) measurements are described for various cellulose preparations (Park et al., 2010), and a description of crystalline properties of plastics is provided by Gilbert (2017a). There is a broad range of crystallinity levels of cellulose and plastics, *e.g.* PVC has low crystallinity of ~10% (Gilbert, 2017a).

9.4.2. Lytic polysaccharide monooxygenase activity towards crystalline cellulose

LPMOs (EC 1.14.99.-) are copper-dependent monooxygenases which were discovered about a decade ago (see Horn et al. (2012) for a historical overview). They are enzymes that can function on a relatively flat substrate surface (Horn et al., 2012; Quinlan et al., 2011). LPMOs are active towards a range of polysaccharides besides cellulose, such as starch, hemicelluloses (*e.g.* xylan) (Couturier et al., 2018) and chitin. LPMOs improve degradation of lignocellulose likely due to their ability to attack bonds that other enzymes (mainly hydrolyases) cannot attack. The crystal structures of LPMOs provide insights into the 3-D structure of these enzymes and how they function on a flat substrate surface (Frandsen and Lo Leggio, 2016). There is still much debate on the preferred LPMO oxygen co-substrate (*e.g.* molecular oxygen versus hydrogen peroxide) and understanding LPMO activity is a major research focus (Eijsink et al., 2019). A recent review on the functional characterisation of LPMOs speculates very briefly that plastics may perhaps be discovered as novel LPMO substrates in the future (Eijsink et al., 2019).

9.4.3. Non-enzymatic fungal strategies for reducing cellulose crystallinity

There are also non-enzymatic strategies used by basidiomycete fungi to degrade cellulose (Baldrian and Valášková, 2008). One of these non-enzymatic approaches is the chelator-mediated Fenton (CMF) system (Hegnar et al., 2019). The CMF system generates hydroxy radicals (that can then attack the cellulose) using chelated iron and hydrogen peroxide. Attempts to biomimic the CMF system (*i.e.* without using a fungus) for pretreatment of lignocellulose have met with limited success (Hegnar et al., 2019). Non-enzymatic Fenton chemistry from a brown-rot fungus was involved in PS-sulfonate degradation (Krueger et al., 2015b). However, degradation of the non-sulfonated PS was low (Krueger et al., 2017).

9.4.4. Dominance of non-biological methods to reduce cellulose crystallinity

The dominance of thermochemical (*i.e.* non-biological) methods in the pretreatment of lignocellulose, which reduces the crystallinity, may be an indication of the difficulties ahead for reducing the crystallinity of plastics by biological routes. The problems are amplified by the longer times required for biological degradation routes which can make the process economically unviable (Baruah et al., 2018). An example of the thermochemical approach is the use of deep eutectic solvents in PET glycolysis (these solvents have similar characteristics to ionic liquids used for the pretreatment of lignocellulosic biomass) (Wang et al., 2015).

9.5. Relevance of gene induction and repression in lignocellulose degradation

What (if anything) could components of plastics directly induce? Besides cutin-derived (if cutin is considered a surrogate for PCL plastic), to our knowledge, there are no examples of direct induction of fungal gene expression by plastic components. Experimental design to understand induction is complex where appropriate controls to quantify secondary or indirect effects are required (*e.g.* a control without a carbon source to account for starvation-related expression that culturing on a plastic likely resembles). In particular, the induction of oxidoreductases is complex often requiring depletion of excess carbon and nitrogen beforehand (Janusz et al., 2013). Notably, carbon and nitrogen (de) repression are also relevant to protease production (Snyman et al., 2019). In theory, carbon and nitrogen repression should not affect plastic degradation as the monomers of plastics are unlikely to be catabolised by fungi and thus affect the main C/N catabolic pathways. But in practice, as the plastic will be a negligible carbon source, the genes involved are likely those used to degrade recalcitrant carbon sources, such as lignocellulose, and thus catabolite repression will likely be a factor in the presence of simpler, easily metabolizable carbon sources.

Cutin and its monomers can function as inducers for cutinases. In *A. nidulans*, two of the four cutinase encoding genes were induced by cutin and its monomers. They also appeared to be regulated by the fatty acid regulator A (FarA) transcription factor (Bermúdez-García et al., 2019). In *Trichoderma*, there are also examples of genes encoding cutinases being induced by cutin monomers, *e.g. Thcut1* from *Trichoderma harzanium* (Rubio et al., 2008). As a model system, the induction of cutinases by plastics may be confounded by how cutinases are part of regulatory cascades related to pathogenesis in plant pathogenic fungi. The use of a saprotrophic fungus not closely related to plant pathogenic fungi could obviate this confounding factor.

Transcriptomics approaches, using microarrays and RNAseq which are applied extensively with lignocellulose degradation by fungi, could be used to indicate which genes appear to be upregulated when fungi are exposed to plastics. Understanding the transcriptional regulation of genes encoding CAZymes (Benocci et al., 2017) such as carbon catabolite repression (CCR) (Adnan et al., 2018) improved CAZyme production. The use of mixed-species cultures (and measurement of expression by dual-RNAseq) can lead to the identification of expression of otherwise silent or lowly expressed genes, *e.g.* using mixed-species cultures of

ascomycete fungi on wheat straw (Daly et al., 2017b). The use of dual-RNAseq with mixed-species cultures on plastics may identify the expression of otherwise silent genes. Because plastic may have simply not existed for long enough for fungi to evolve any specific transcriptional responses, transcriptomic comparisons of induction on plastic compared to a non-plastic control may not be particularly informative. Instead, a transcriptomic comparison between plastic and non-plastic degrading strains may be more informative *e.g.,* a transcriptomic comparison of the PU-degrading *A. tubingensis* strain to non-plastic degrading *A. tubingensis* strains.

9.6. Random mutagenesis and adaptive laboratory-based evolution

Random induced mutations such as by UV or chemical mutagenesis can improve the desired properties of fungal strains, *e.g.* random mutagenesis of *T. reesei* led to higher cellulase secretion levels (Peterson and Nevalainen, 2012). Adaptive laboratory-based evolution of fungi involves spontaneous mutations occurring that lead to improved growth on the condition of interest (de Vries et al., 2018). Two examples of adaptive laboratory-based evolution are for improving cellulase production (Patyshakuliyeva et al., 2016) or increased tolerance to aromatic compounds (Lubbers et al., 2020) in *A. niger*. The sparsity of reports on the application of these techniques to plastic degradation by fungi suggests these techniques may have limited applicability to plastic degradation or perhaps have not yet been attempted.

9.7. Enzyme cocktail development and industrial scale-up

Apart from in *situ* plastic degradation by fungi, some of the above approaches could lead to the identification or engineering of enzymes that could be used as part of an enzyme cocktail to degrade plastics. A substantial part of research on lignocellulose degradation concerns the development and optimisation of enzyme cocktails, *e.g.* the minimal enzyme concept for biomass processing concerns itself with replacing crude enzyme cocktails with the minimum number of required activities for degradation of a polymer (Meyer et al., 2009). Techno-economic analysis of scale-up to production levels has been extensively studied for lignocellulose degrading enzymes, *e.g.* predicting the costs of enzyme production (Klein-Marcuschamer et al., 2012). Besides the development of enzyme cocktails, whole organism methods (*e.g.* biological pretreatment) should be explored, as there has been success in the pretreatment of lignocellulose for downstream paper and ethanol production (with significant reductions in capital expenditure) (Giles et al., 2015).

10. Comparative genomics, bio-prospecting and plastic degradation

Research on lignocellulose degradation by fungi has a track record of linking genotype to phenotype. Comparative genomics has been critical for explaining the genetic basis for lignocellulose degradation phenotypes, *e.g.* how white-rot fungal genomes encode Class II peroxidases that are few in or absent from brown-rot fungal genomes (Floudas et al., 2012; Grigoriev et al., 2014). Also, sequencing of the genomes of the most common *Trichoderma* species demonstrates how genomics can be correlated with phenotypes (Kubicek et al., 2019). There is potential for breakthroughs by screening for plastic degradation and sequencing genomes of plastic degraders and non-degraders to correlate phenotypes with genomics.

Bioprospecting for cutinases with increased plastic degrading activity is a promising field, *e.g.* screening for cutinase and plastic degrading activities from epiphytes found on highly waxy leaf surfaces (Fig. 6) and performing comparative genomics. Cutinase enzymes have been extensively studied for phytopathogenicity but also increasingly for plastic degradation (Ferrario et al., 2016). One seminal example is a cutinase from *A. oryzae* that degrades the biodegradable plastics PBS and PBSA (Maeda et al., 2005). The ability of cutinases to function in the

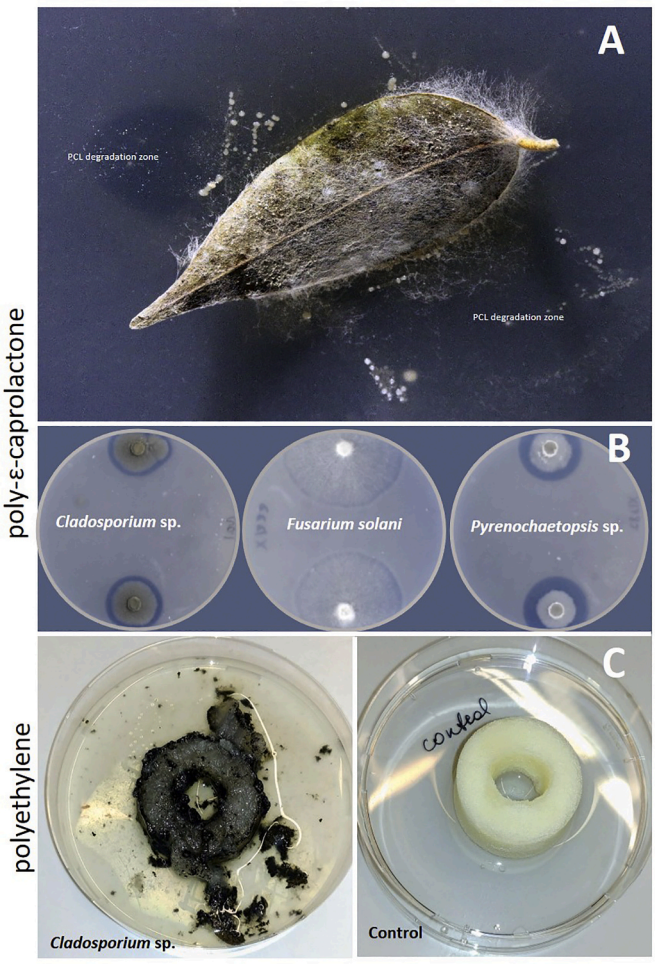

Fig. 6. Screening for fungi capable to degrade plastics. A. Natural epiphytic fungi on a highly waxy leaf of *Ficus* sp. incubated on the agar plate supplemented with the powder of the biodegradable plastic (PCL) and antibiotics preventing the growth of bacteria. The clearance zones on the agar medium indicate the presence of potentially positive strains. In this set up, the leaf is used as a source of nutrients and as a potential inducer of cutinolytic activity. B. Pure fungal culture isolated from plates as shown on A and cultivated on PCL as the only source of nutrients. Note, the growth is probably supported by the nutrients reserved in the agar plug. The clearance zone around each colony corresponds to the ability to degrade PCL. C. Polyethylene sponge degraded by *Cladosporium* sp. isolated in B after three weeks of incubation in a wet chamber at 25 °C in darkness (left) compared to the control (right).

degradation of plastics likely relates to the similarity of the two cutin monomer units to the trimer of the biodegradable plastic polycaprolactone (Pathak and Navneet, 2017). Apart from the highly biodegradable plastics, cutinases can degrade recalcitrant petroleum-based plastics such as PET as described in other sections of this review (*e.g.* Table 3).

11. Regulatory hurdles and biosafety

Another benefit of using techniques and research on lignocellulose degradation for plastic degradation is that this approach could be informative for biosafety risk assessments. A key factor for regulatory approval could be to assess engineered fungi for plastic degradation from the perspective of lignocellulose degradation, *e.g.* if a strain is modified for improved plastic degradation, whether there could be increased or emergent virulence needs to be assessed (by how the engineered fungus also degrades plant cell walls). The avoidance of unintentionally producing microbes with increased pathogenicity (de

Lorenzo, 2010) can be aided by connecting plastic degradation and lignocellulose degradation.

The use of genetically modified organisms (GMOs) presents a regulatory hurdle to overcome, particularly in the European Union. "Markerless" technologies such as used in many of the implementations of CRISPR-Cas9 could overcome some of these regulatory hurdles in jurisdictions that do not consider a CRISPR-Cas9 edited fungus as a GMO (Idnurm and Meyer, 2018). However, performing this biosafety risk assessment nonetheless seems a prudent approach in light of the potential from improved plastic-degrading fungi for emergent virulence towards plants or interference with the natural carbon cycle (*e.g.* inadvertently engineering a super-saprotrophic fungus).

12. Conclusions

There is a wealth of methods developed for understanding lignocellulose degradation that could be applied to plastic degradation. Methods that could be more readily employed include the microscopic visualisation techniques and approaches to overcome hydrophobicity such as using amphiphilic molecules. Methods such as transcriptomics to understand gene induction and repression may not be readily applied to fungal plastic degradation because plastic has simply not existed for long enough for fungi to evolve responses to plastics. Thus, random mutagenesis and laboratory evolution approaches must be used with fungi. Suppose fungi cannot be directly used for degradation of recalcitrant plastics in the near future. In that case, they could at least function to obviate the need for physical pretreatment such as size reduction of biodegradable plastics, *e.g.* da Luz et al. (2013).

Declaration of Competing Interest

All authors are declare that they have no actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations within five years of beginning the submitted work that could inappropriately influence, or be perceived to influence, their work..

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