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Plant-Polysaccharide-Degrading Enzymes from Basidiomycetes

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SUMMARY

Basidiomycete fungi subsist on various types of plant material in diverse environments, from living and dead trees and forest litter to crops and grasses and to decaying plant matter in soils. Due to the variation in their natural carbon sources, basidiomycetes have highly varied plant-polysaccharide-degrading capabilities. This topic is not as well studied for basidiomycetes as for ascomycete fungi, which are the main sources of knowledge on fungal plant polysaccharide degradation. Research on plant-biomass-decaying fungi has focused on isolating enzymes for current and future applications, such as for the production of fuels, the food industry, and waste treatment. More recently, genomic studies of basidiomycete fungi have provided a profound view of the plant-biomass-degrading potential of wood-rotting, litter-decomposing, plant-pathogenic, and ectomycorrhizal (ECM) basidiomycetes. This review summarizes the current knowledge on plant polysaccharide depolymerization by basidiomycete species from diverse habitats. In addition, these data are compared to those for the most broadly studied ascomycete genus, *Aspergillus*, to provide insight into specific features of basidiomycetes with respect to plant polysaccharide degradation.

INTRODUCTION

Plant biomass is the most abundant renewable carbon source on Earth. Many microbes have central roles in the degradation of this biomass to ensure a global carbon cycle. Fungi are special-

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ized to use plant biomass as a carbon source by producing enzymes that degrade plant cell wall polysaccharides into metabolizable sugars. Plant-polysaccharide-depolymerizing enzymes are of great interest to biotechnology, as the products of their catalysis can be used as precursors in the processes that generate bio-based products, e.g., fuels, paper, food, animal feed, and chemicals (1). The enzymes degrading or modifying plant polysaccharides are classified as carbohydrate-active enzymes (CAZymes) and are divided into families according to their amino acid sequence and structural similarity (2). The CAZy database (http://www.cazy.org/) is organized into families of glycoside hydrolases (GHs), carbohydrate esterases (CEs), polysaccharide lyases (PLs), glycosyltransferases (GTs), and auxiliary activities (AA) (2).

Basidiomycetes colonize or inhabit a diversity of plant material in forests, meadows, farmlands, and compost. Different species have various CAZyme sets to meet the needs of their ecological roles as saprobes (wood-rotting and litter-decomposing fungi), symbionts and endophytes (mycorrhizas and lichens), parasites, and plant and animal pathogens (3, 4). Basidiomycetes are the most efficient degraders of woody biomass (5) and therefore are essential for the global carbon cycle. The understanding of the mechanisms that basidiomycetes use for plant polysaccharide degradation is in its infancy compared to ascomycete studies, due largely to the traditional and well-established industrial relevance of several ascomycetes. Since the enzyme sets of basidiomycetes are likely to reflect adaptation to their unique natural niches, basidiomycetes contain a huge potential for applications in various industries, which has so far remained largely unexplored.

As mentioned above, our knowledge of basidiomycetes regarding their ability to decompose plant polysaccharides is limited compared to the wealth of information on ascomycetes. Before the genomics era, functional analyses of purified enzymes and expression studies of the corresponding genes were the main approaches for characterization of the fungal CAZyme machinery. However, these methods are laborious and cannot provide a full overview of a fungal CAZyme arsenal. More detailed insights into the entire polysaccharide-degrading capability of fungi with interesting ecologies have been obtained through genome sequencing (6–15) together with transcriptome and proteome analyses (16–18). However, only by combining these omics data with biochemical characteristics of the enzymes can we complete our understanding of the plant cell wall polysaccharide degradation ability of basidiomycete fungi.

This review explores the enzymatic potential of basidiomycetes from different biotopes and focuses on their ability to depolymerize cellulose, hemicelluloses, and pectin. The basidiomycetes are compared to species belonging to *Aspergillus*, which is one of the most extensively studied ascomycete genera, to dissect differences in their strategies for plant polysaccharide degradation. While there is also a large diversity among the ascomycete fungi, the aspergilli are among the few ascomycetes that have been studied with respect to the degradation of all plant polysaccharides (19). First, a comparison of the putative CAZyme-encoding genes found in the genomes of wood- and litter-decomposing basidiomycetes, plant pathogens, and ectomycorrhizal (ECM) fungi gives insight into their plant cell wall polysaccharide-degrading enzyme potential. Second, previously characterized CAZymes isolated from basidiomycetes are compared to those from genomic studies. Finally, the so far poorly addressed regulatory mechanisms of basidiomycetes in plant cell wall degradation are reviewed.

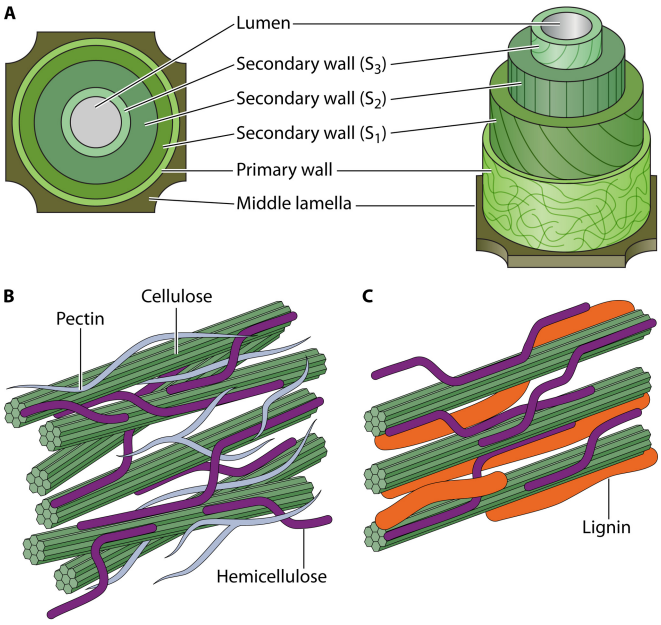

FIG 1 Simplified model of plant cell wall structure. (A) The structure consists of three main layers: the middle lamella and the primary and secondary walls. (A and B) The main polysaccharides and lignin which form the surrounding structure for the plasma membrane are presented in the primary (B) and secondary wall (C). The lignin content in the primary cell wall (not illustrated) varies considerably depending on the plant species (Table 1). The illustrations are not to scale.

PLANT CELL WALL POLYSACCHARIDES

The three most important polysaccharide building blocks of plant cell walls are cellulose, hemicellulose, and pectin. Together with lignin, an aromatic heteropolymer, they form a degradation-resistant and functional complex that provides rigidity and structure to the plant and protects the cells from microbial attack. The plant cell wall consists of three main layers: the middle lamella and the primary and secondary walls (Fig. 1A) (20, 21). Each of these layers has a unique structure and chemical composition that also differ strongly between plant species, tissues, and the growth phase of the plant (Fig. 1B and C).

The major differences in the chemical compositions of softwood (e.g., pine and spruce) and hardwood (e.g., birch, aspen, and oak) are in the structure and content of hemicelluloses (Table 1). Hemicelluloses in softwood consist mainly of galactoglucomannans, whereas the majority of hardwood hemicelluloses are glucuronoxylans (Table 1) (20). On average, softwood has higher lignin content than hardwood, while the amount of cellulose in softwood is smaller than that in hardwood (Table 1) (20).

The chemical compositions of cell walls in flowering plants also vary (Table 1). Monocots, i.e., grasses, are considered the most important renewable-energy crops, and their primary cell wall consists mainly of cellulose and hemicelluloses, whereas their secondary walls contain larger amounts of cellulose, a different composition of hemicelluloses, and significant amounts of lignin (Table 1) (22). The primary cell walls of dicots differ from those of grasses by their low xylan and high xyloglucan and mannan con-

TABLE 1 Approximate chemical compositions of softwood, hardwood, monocot, and dicot plant cell walls[a]

Plant material	Chemical composition (% dry wt)[b]						
		Hemicelluloses					
	Cellulose	Mannan	Xylan	β-Glucan	Xyloglucan	Pectin	Lignin
Softwood	33–42	10–15	5–11	—	—	—	27–32
Hardwood	38–47	2–5	15–30	—	—	—	21–31
Monocots							
Primary	20–30	Minor	20–40	10–30	1–5	5	Minor
Secondary	35–45	Minor	40–50	Minor	Minor	Minor	20
Dicots							
Primary	15–30	5–10	5	ND	20–25	20–30	Minor
Secondary	45–50	3–5	20–30	ND	Minor	Minor	7–10

[a] Data were obtained from references 20 and 22.
[b] —, not reported; ND, not detected.

tents (Table 1) (22). In addition, the amount of pectin is notably larger in dicots than in grasses (Table 1). The secondary wall of dicots is composed of cellulose, hemicelluloses, and lignin (Table 1) (22).

Cellulose

Cellulose, found in both the primary and secondary cell walls, is the most abundant polysaccharide in plant matter (40 to 45% dry weight) and gives the plant cell wall its rigid structure (20). Repeating units of β-1,4-linked D-glucose form linear cellulose chains, which are held together by intermolecular hydrogen bonds and create linear crystalline structures (microfibrils) (23) and less crystalline, amorphous regions. The ratio of crystalline to amorphous regions varies between the layers of primary and secondary cell walls as well as between plant species. Cellulose microfibrils are more irregularly ordered in the outer layer than in the inner layer of the primary cell wall, where they are perpendicularly oriented (Fig. 1). Furthermore, the angles and directions of the cellulose microfibrils vary among the three sublayers (sublayer 1 [S_1] to S_3) of the secondary plant cell wall (20, 21).

Hemicellulose

Hemicelluloses (20 to 30% plant dry weight) support the structure of the cellulose microfibrils in the primary and secondary walls of plant cells (20). There are four types of amorphous hemicellulose structures with different main monosaccharide units in their hemicellulose backbone. Xylan is the most common hemicellulose polymer with a β-1,4-linked D-xylose backbone. Other hemicelluloses are xyloglucan (β-1,4-linked D-glucose), found mainly in the primary walls; β-glucan (β-1,3;1,4-linked D-glucose); and mannan (β-1,4-linked D-mannose) (21). Xylan, xyloglucan, and mannan backbones are decorated with branched monomers and short oligomers consisting of D-galactose, D-xylose, L-arabinose, L-fucose, D-glucuronic acid, acetate, ferulic acid, and *p*-coumaric acid that are cleaved by debranching enzymes (24).

Pectin

Pectin is a noncellulosic polysaccharide containing galacturonic acid that provides additional cross-links between the cellulose and hemicellulose polymers. It is found mainly in plant primary cell walls and middle lamella (25). The pectin concentration in the middle lamella is high at an early stage of plant growth, but the concentration decreases during lignification (20). The simplest pectin structure is homogalacturonan (HG), which is a linear polymer of α-1,4-linked D-galacturonic acid residues that can be methylated at the C-6 carboxyl group and acetylated at the O-2 or O-3 position. Xylogalacturonan (XGA) is a substituted galacturonan that has β-1,3-linked D-xylose residues attached to the galacturonic acid backbone. The second substituted galacturonan is rhamnogalacturonan II (RG-II). The structure of RG-II is more complex than the structure of XGA. Altogether, 12 different glycosyl residues, e.g., 2-*O*-methyl xylose, 2-*O*-methyl fucose, aceric acid, 2-keto-3-deoxy-D-lyxo heptulosaric acid, and 2-keto-3-deoxy-D-manno-octulosonic acid, can be attached to the galacturonic acid backbone (25). The most complex pectin structure, rhamnogalacturonan I (RG-I), has a backbone of alternating D-galacturonic acid and L-rhamnose residues, with branching structures consisting of D-galactose and L-arabinose chains attached to the L-rhamnose residues.

ENZYMES MODIFYING PLANT POLYSACCHARIDES

An overview of the known fungal plant-polysaccharide-degrading or -modifying enzymes is presented in Table 2. The enzymes are divided according to their substrates, and their EC numbers, abbreviations, and corresponding CAZyme families (2) are also shown.

Cellulose Degradation

The main enzymes that hydrolyze cellulose, so-called classical cellulases, are endoglucanases, exoglucanases, and β-glucosidases (BGLs). β-1,4-Endoglucanase (EG) (EC 3.2.1.4) cleaves within the cellulose chains to release glucooligosaccharides (Fig. 2A). Exoglucanases or cellobiohydrolases (CBHs) release cellobiose from the end of the cellulose chains. The two types of cellobiohydrolases, CBHI and CBHII (EC 3.2.1.176 and EC 3.2.1.91, respectively), degrade cellulose from either the reducing or the nonreducing end, respectively, with different processivities, i.e., the efficiency of the sequential hydrolysis of the β-1,4-glycosidic bonds by the cellulase before the dissociation of the enzyme from the substrate (26). BGL (EC 3.2.1.21) releases the smallest unit, glucose, from shorter oligosaccharides.

Recently, oxidoreductive cleavage of the cellulose chain has been reported. Cellobiose dehydrogenase (CDH) (EC 1.1.99.18)

TABLE 2 Plant-polysaccharide-degrading enzymes

Substrate	Enzyme activity	EC no.[a]	Abbreviation	CAZyme family(ies)
Cellulose	β-1,4-Endoglucanase	3.2.1.4	EG	GH3, -5, -6, -7, -9, -12, -45
	Cellobiohydrolase (reducing end)	3.2.1.176	CBHI	GH7
	Cellobiohydrolase (nonreducing end)	3.2.1.91	CBHII	GH6
	β-1,4-Glucosidase	3.2.1.21	BGL	GH1, -3
	Cellobiose dehydrogenase	1.1.99.18	CDH	AA3_1, AA8
	Lytic polysaccharide monooxygenase	NA	LPMO	AA9
Xylan	β-1,4-Endoxylanase	3.2.1.8	XLN	GH10, -11
	Xylobiohydrolase	3.2.1.–	XBH	
	β-1,4-Xylosidase	3.2.1.37	BXL	GH3, -43
Galactomannan	β-1,4-Endomannanase	3.2.1.78	MAN	GH5, -26
	β-1,4-Mannosidase	3.2.1.25	MND	GH2
	β-1,4-Galactosidase	3.2.1.23	LAC	GH2, -35
	α-1,4-Galactosidase	3.2.1.22	AGL	GH27, -36
	α-Arabinofuranosidase	3.2.1.55	ABF	GH51, -54
	Galactomannan acetyl esterase	3.1.1.–	GMAE	
Xyloglucan	Xyloglucan β-1,4-endoglucanase	3.2.1.151	XEG	GH12, -74
	α-Arabinofuranosidase	3.2.1.55	ABF	GH51, -54
	α-Xylosidase	3.2.1.177	AXL	GH31
	α-Fucosidase	3.2.1.51	AFC	GH29, -95
	α-1,4-Galactosidase	3.2.1.22	AGL	GH27, -36
	β-1,4-Galactosidase	3.2.1.23	LAC	GH2, -35
Arabinoxylan	Arabinoxylan arabinofuranohydrolase/arabinofuranosidase	3.2.1.55	AXH	GH62
	α-Glucuronidase	3.2.1.139	AGU	GH67, -115
	α-1,4-Galactosidase	3.2.1.22	AGL	GH27, -36
	β-1,4-Galactosidase	3.2.1.23	LAC	GH2, -35
	Acetyl xylan esterase	3.1.1.72	AXE	CE1, -5
	Feruloyl esterase	3.1.1.73	FAE	CE1
Pectin	Endopolygalacturonases	3.2.1.15	PGA	GH28
	Exopolygalacturonases	3.2.1.67	PGX	GH28
	Xylogalacturonan hydrolase	3.2.1.–	XGH	
	Endorhamnogalacturonase	3.2.1.171	RHG	GH28
	Exorhamnogalacturonase	3.2.1.–	RHX	GH28
	Rhamnogalacturonan rhamnohydrolase	3.2.1.174	RGXB	GH28
	α-Rhamnosidase	3.2.1.40	RHA	GH78
	α-Arabinofuranosidase	3.2.1.55	ABF	GH51, -54, -62
	Endoarabinanase	3.2.1.99	ABN	GH43
	Exoarabinanase	3.2.1.–	ABX	GH93
	β-1,4-Endogalactanase	3.2.1.89	GAL	GH53
	Unsaturated glucuronyl hydrolase	3.2.1.–	UGH	GH88
	Unsaturated rhamnogalacturonan hydrolase	3.2.1.172	URH	GH105
	β-1,4-Xylosidase	3.2.1.37	BXL	GH3, -43
	β-1,4-Galactosidase	3.2.1.23	LAC	GH2, -35
	Pectin lyase	4.2.2.10	PEL	PL1
	Pectate lyase	4.2.2.2	PLY	PL1, -3, -9
	Rhamnogalacturonan lyase	4.2.2.23	RGL	PL4, -11
	Pectin methyl esterase	3.1.1.11	PME	CE8
	Pectin acetyl esterase	3.1.1.–	PAE	
	Rhamnogalacturonan acetyl esterase	3.1.1.–	RGAE	CE12
	Feruloyl esterase	3.1.1.73	FAE	CE1

[a] NA, not categorized by the International Union of Biochemistry and Molecular Biology (IUBMB).

and lytic polysaccharide monooxygenases (LPMOs) participate in cellulose degradation in combination with cellulases (Fig. 2A) (27, 28). CDH is the only known extracellular flavocytochrome that oxidizes cellobiose and cellooligosaccharides to the corresponding lactones (29, 30). The exact role of CDH in lignocellulose degradation is still unclear, although there is evidence of its relevance in both the cellulolytic and lignin-modifying machinery of fungi (29, 30). The ability of CDH to produce hydroxyl radicals through Fenton chemistry supports its role in lignin modification, while oxidation of cellobiose together with the production of electrons for LPMO-catalyzed cellulose depolymerization demonstrate the participation of CDH in the degradation of cellulose (29, 31, 32).

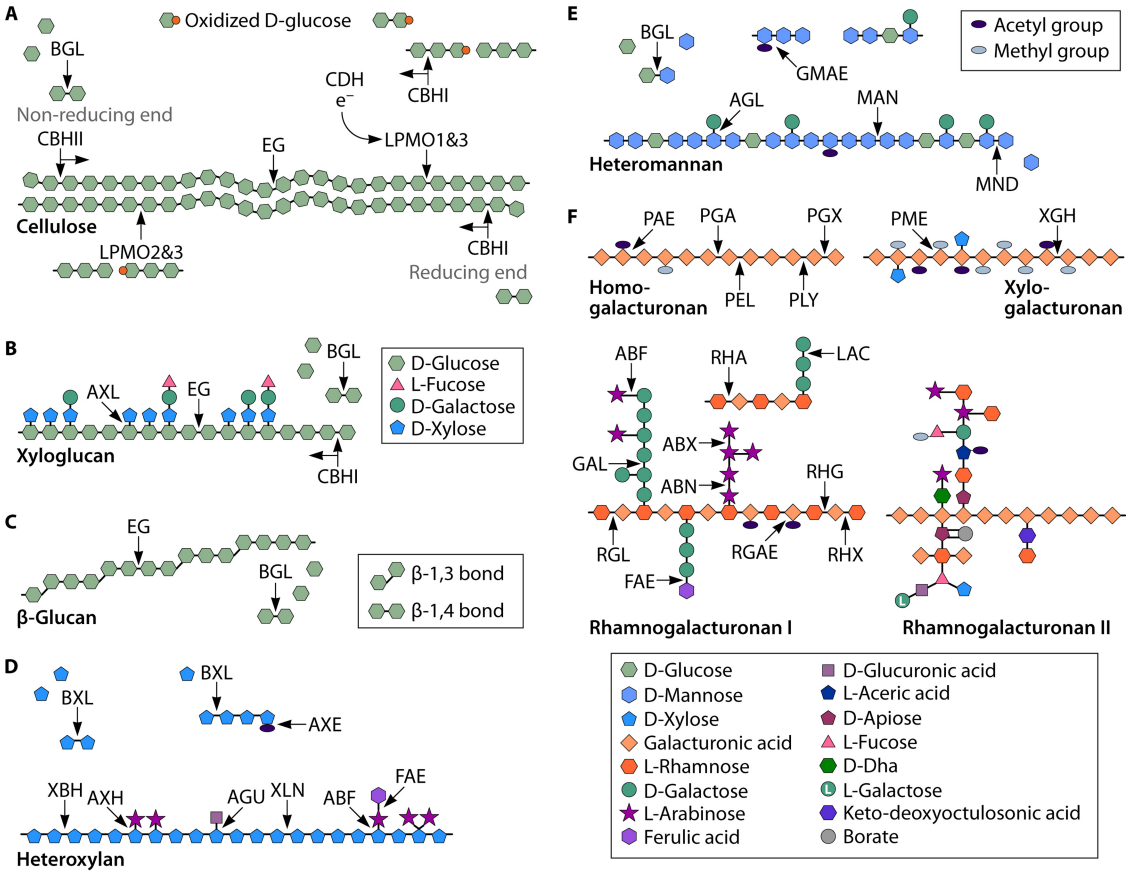

FIG 2 Schematic representation of plant cell wall polysaccharides and selected corresponding polysaccharide-degrading enzymes. (A) Cellulose; (B) xyloglucan; (C) β-glucan; (D) heteroxylan; (E) heteromannan; (F) pectin. Enzyme abbreviations are presented in Table 2. Polysaccharide structures were drawn by using data reported previously by Mohnen (203) and Doblin et al. (204).

LPMOs are copper monooxygenases that catalyze the direct oxidation of the cellulose chain leading to cleavage of the glycosidic bond (28, 31, 32). Moreover, fungal LPMOs can be divided into at least three classes according to their sequence similarity and specific activities toward cellulose (33). Type 1 LPMOs catalyze oxidation of the glucose unit at the C-1 position, resulting in the formation of aldonic acids at the reducing end of the cellulose chain (28, 32). Type 2 LPMOs generate ketosugars at the nonreducing end of the cellulose chain by oxidizing at the C-4 position (34). LPMOs of type 3 are not as specific as type 1 or 2 enzymes, and they are able to oxidize both positions (32). Oxidation at C-6 has also been proposed (28). The reaction catalyzed by LPMOs requires an electron donor to reduce copper II to copper I in the active site of the enzyme and molecular oxygen to form the copper-oxygen complex, which is capable of oxidizing the glycosidic bond (35). In addition to the above-mentioned CDH, other naturally occurring electron donors for LPMOs have been proposed, e.g., gallic acid or lignin (28, 36). Also, several compounds, e.g., ascorbic acid, have been shown to act as reductants in LPMO catalysis *in vitro* (28, 34).

Hemicellulose Degradation

Due to variable structures, a specific set of CAZymes is needed to degrade the backbone and branching structures of each hemicellulose (Fig. 2B to E) (37). The xylan backbone is cleaved by β-1,4-endoxylanase (XLN) (EC 3.2.1.8) into shorter oligomers (Fig. 2D). A xylobiohydrolase that hydrolyzes xylan into xylobiose has also been described (38). β-1,4-Xylosidase (BXL) (EC 3.2.1.37) hydrolyzes xylobiose into its monomeric units and also releases D-xylose from larger xylooligosaccharides from the nonreducing terminus (24, 39). The xyloglucan backbone, the structure of which is similar to that of cellulose, is hydrolyzed by EGs, CBHs, and BGLs (Fig. 2B) (24). β-Glucan can be degraded by EGs into oligosaccharides (Fig. 2C). The β-1,4-linked D-mannose backbone of mannan is cleaved by β-1,4-endomannanase (MAN) (EC 3.2.1.78) to mannooligosaccharides (Fig. 2E). β-1,4-Mannosidase (MND) (EC 3.2.1.25) releases D-mannose from the terminal ends of mannan (24). In addition, BGL acts on the galactoglucomannan backbone.

The enzymatic oxidative cleavage of hemicelluloses was recently confirmed (40). First, the ability of CDH to accept electrons from xylooligosaccharides and interact with various LPMOs was detected, suggesting that these enzymes are able to act on hemicelluloses (41). Recently, LPMO9C of the ascomycete fungus *Neurospora crassa* was shown to cleave xyloglucan, β-glucan, and, to a lesser extent, glucomannan with ascorbic acid as a reductant (40).

Pectin Degradation

Endopolygalacturonases (PGAs) (EC 3.2.1.15) and exopolygalacturonases (PGXs) (EC 3.2.1.67) act within and at the terminal end

of the α-1,4-linked D-galacturonic acid polymer, respectively, releasing D-galacturonic acid from the homogalacturonan backbone (Fig. 2F). Xylogalacturonan is cleaved specifically by xylogalacturonan hydrolases (XGHs) (EC 3.2.1.–). The backbone of rhamnogalacturonan I is hydrolyzed by exorhamnogalacturonase (RHX) (EC 3.2.1.–), endorhamnogalacturonase (RHG) (EC 3.2.1.171), rhamnogalacturonan rhamnohydrolase (RGXB) (EC 3.2.1.174), and α-rhamnosidase (RHA) (EC 3.2.1.40) (19, 24).

Pectin lyase (PEL) (EC 4.2.2.10), pectate lyase (PLY) (EC 4.2.2.2), and rhamnogalacturonan lyase (RGL) (EC 4.2.2.23) also cleave the pectin backbone, using a β-elimination mechanism. Lyases have different sensitivities to the acetylations (O-2 or O-3) or methyl esterifications (O-6) of the D-galacturonic acid backbone. In contrast to pectate lyases, pectin lyases prefer substrates with a high degree of methyl esterification. Rhamnogalacturonan lyases favor nonacetylated substrates (19, 24).

Debranching Enzymes

The enzymes described above cleave the main chains of cellulose and the backbone and branches of hemicellulose and pectin. However, smaller side branches extending from hemicellulose and pectin require a different set of CAZymes. The debranching enzymes (also known as accessory enzymes) α-D-xylosidase (AXL) (EC 3.2.1.177), α-L-arabinofuranosidase (ABF) (EC 3.2.1.55), arabinoxylan arabinofuranohydrolase (AXH), endoarabinase (ABN), exoarabinase (ABX), α-D-galactosidase (AGL) (EC 3.2.1.22), β-D-galactosidase (LAC) (EC 3.2.1.23), endogalactanase (GAL) (EC 3.2.1.89), exogalactanase (EC 3.2.1.–), α-glucuronidase (AGU) (EC 3.2.1.139), feruloyl esterase (FAE) (EC 3.1.1.73), *p*-coumaroyl esterase (*p*CAE) (EC 3.1.1.–), acetyl xylan esterase (AXE) (EC 3.1.1.72), galactomannan acetyl esterase (GMAE) (EC 3.1.1.–), rhamnogalacturonan acetyl esterase (RGAE) (EC 3.1.1.–), pectin acetyl esterase (PAE) (EC 3.1.1.–), and pectin methyl esterase (PME) (EC 3.1.1.11) work synergistically with the main-chain-depolymerizing enzymes to degrade plant polysaccharides (19).

BASIDIOMYCETE GENOMES AND PLANT POLYSACCHARIDE DEGRADATION

To date, an increasing number of basidiomycete genomes have been sequenced and annotated to understand fungal physiology and, in several cases, to search for enzymes of interest that could be of use in industrial applications (Table 3) (42). These fungi inhabit a wide range of ecological niches and colonize various growth substrates, such as conifers, deciduous trees, forest litter, crops, grassland soils, and roots of plants. Differences in the CAZyme sets can often be linked to fungal habitat. For example, the wood-decaying white rot fungus *Phanerochaete chrysosporium* has a larger repertoire of plant cell wall polysaccharide-degrading enzymes than the biotrophic phytopathogen *Ustilago maydis*, which possesses a minimal set of CAZyme-encoding genes in order to prevent host plant defense responses, as suggested in previous studies (6, 8). While it cannot be automatically concluded that an increase in the number of genes related to a particular polysaccharide also means an improved degradation of this polysaccharide, many studies have revealed such correlations (43–50). However, there are also clear exceptions to this. The most noteworthy exception is the ascomycete *Hypocrea jecorina* (anamorph *Trichoderma reesei*), which is a very efficient cellulose degrader but contains a relatively small number of cellulase-encoding genes in each genome. Its strategy appears to have focused on high production levels of a limited set of enzymes rather than expanding its enzyme repertoire (51). This approach appears to be used by only a minority of fungi, based on an extensive correlation analysis between genome content and growth on plant biomass substrates of >150 fungal species (R. P. de Vries, A. Wiebenga, M. Zhou, P. M. Coutinho, and B. Henrissat, unpublished data).

Wood-Rotting Fungi

Wood-rotting fungi are traditionally divided into white rot and brown rot fungi according to the modification that they cause to wood residue during decay. White rot fungi degrade both lignin and wood polysaccharides (cellulose and hemicelluloses) so that the residual wood is white or yellowish, moist, soft, and often fiber-like. More than 90% of all known wood-rotting basidiomycetes are of the white rot type (52), and they are found more commonly on angiosperm than on gymnosperm wood species in nature. Brown rot fungi degrade wood to yield brown, typically cubical cracks that are easily broken down. Less than 10% of all known wood-decaying basidiomycete species are classified into this group, which occurs most often on gymnosperm wood (53). Interestingly, the analyzed genome sequence data show that many cellulases of wood-rotting basidiomycetes lack the cellulose binding modules (CBMs) generally considered essential for efficient cellulose hydrolysis (54). More sequence data are needed to clarify possible ecological and evolutionary advantages for the occurrence of CBM-less cellulases and other polysaccharide-degrading enzymes in nature.

Genome information indicates that brown rot fungi evolved several times from ancestor white rot species (11). Thus, individual brown rot species may have different sets of characteristics left, which makes this group rather heterogeneous, and some of them resemble white rot fungi. Genome studies of wood-inhabiting basidiomycetes show that there is a need for a more detailed classification of the rot types, since some fungi, e.g., *Botryobasidium botryosum* and *Jaapia argillacea*, do not fulfill the traditional criteria for dichotomous grouping (55). However, it has been suggested that the definition "white rot" should be reserved for those fungi that degrade all cell wall polymers through the action of the lignin-modifying peroxidases and have enzymes capable of attacking crystalline cellulose (55).

White rot fungi. White rot fungi are efficient degraders of the aromatic polymer lignin and cause a characteristic white appearance on degraded wood (56). White rot fungi also have the most extensive arsenal of putative CAZymes among the basidiomycetes (Table 4), allowing them to colonize a wide range of plants, from pine trees to poplars and grapevines (11). White rot fungi make up the majority of wood-rotting basidiomycetes, and the most intensively studied species are commonly isolated from hardwoods (56), which have slightly higher cellulose and hemicellulose (glucomannan and glucuronoxylan) contents than do softwoods (Table 1) (20).

Based on the sequenced genomes (Table 3), the white rot basidiomycetes harbor an extensive set of genes encoding putative cellulolytic enzymes. Genes encoding GH family 6 (GH6) and GH7 enzymes, which include mainly cellulose-hydrolyzing CBHs, are typically present with 1 to 7 copies in all white rot fungal species sequenced so far (Table 4). As an exception, *Pleurotus ostreatus* harbors 16 putative GH7-encoding genes (Table 4). Several genes from GH3 and GH5 (6 to 17 and 16 to 43 genes, respec-

TABLE 3 List of basidiomycete species with published genomes and CAZyme annotations

Ecology	Species	Website(s)	Reference(s)
White rot	*Auricularia subglabra*	http://genome.jgi.doe.gov/Aurde3_1/Aurde3_1.home.html	11
	Bjerkandera adusta	http://genome.jgi.doe.gov/Bjead1_1/Bjead1_1.home.html	205
	Ceriporiopsis (*Gelatoporia*) *subvermispora*	http://genome.jgi.doe.gov/Cersu1/Cersu1.home.html	12
	Dichomitus squalens	http://genome.jgi-psf.org/Dicsq1/Dicsq1.home.html	11
	Fomitiporia mediterranea	http://genome.jgi-psf.org/Fomme1/Fomme1.home.html	11
	Ganoderma lucidum	http://www.herbalgenomics.org/galu/	14
	Ganoderma sp.	http://genome.jgi.doe.gov/Gansp1/Gansp1.home.html	205
	Heterobasidion irregulare	http://genome.jgi-psf.org/Hetan2/Hetan2.home.html	66
	Phanerochaete carnosa	http://genome.jgi.doe.gov/Phaca1/Phaca1.home.html	45
	Phanerochaete chrysosporium	http://genome.jgi-psf.org/Phchr2/Phchr2.home.html	6, 57
	Phlebia brevispora	http://genome.jgi.doe.gov/Phlbr1/Phlbr1.home.html	205
	Pleurotus ostreatus	http://genome.jgi.doe.gov/PleosPC15_2/PleosPC15_2.home.html	55
	Punctularia strigosozonata	http://genome.jgi-psf.org/Punst1/Punst1.home.html	11
	Stereum hirsutum	http://genome.jgi-psf.org/Stehi1/Stehi1.home.html	11
	Trametes versicolor	http://genome.jgi-psf.org/Trave1/Trave1.home.html	11
White rot-like	*Schizophyllum commune*	http://genome.jgi-psf.org/Schco3/Schco3.home.html	15
Uncertain classification	*Botryobasidium botryosum*	http://genome.jgi.doe.gov/Botbo1/Botbo1.home.html	55
	Jaapia argillacea	http://genome.jgi.doe.gov/Jaaar1/Jaaar1.home.html	55
Brown rot	*Coniophora puteana*	http://genome.jgi-psf.org/Conpu1/Conpu1.home.html	11
	Dacryopinax sp.	http://genome.jgi-psf.org/Dacsp1/Dacsp1.home.html	11
	Fomitopsis pinicola	http://genome.jgi-psf.org/Fompi3/Fompi3.home.html	11
	Gloeophyllum trabeum	http://genome.jgi-psf.org/Glotr1_1/Glotr1_1.home.html	11
	Postia placenta	http://genome.jgi-psf.org/Pospl1/Pospl1.home.html	18
	Serpula lacrymans S7.3	http://genome.jgi-psf.org/SerlaS7_3_2/SerlaS7_3_2.home.html	71
	Serpula lacrymans S7.9	http://genome.jgi-psf.org/SerlaS7_9_2/SerlaS7_9_2.home.html	71
	Wolfiporia cocos	http://genome.jgi-psf.org/Wolco1/Wolco1.home.html	11
Litter decomposing	*Agaricus bisporus* var. *bisporus*	http://genome.jgi-psf.org/Agabi_varbisH97_2/Agabi_varbisH97_2.home.html	9
	Agaricus bisporus var. *burnettii*	http://genome.jgi.doe.gov/Agabi_varbur_1/Agabi_varbur_1.home.html	9
	Galerina marginata	http://genome.jgi.doe.gov/Galma1/Galma1.home.html	55
Straw decomposing	*Volvariella volvacea*	http://www.ncbi.nlm.nih.gov/genome/?term=Volvariella+volvacea	13
Coprophilic	*Coprinopsis cinerea*	http://genome.jgi-psf.org/Copci1/Copci1.home.html	206
Plant pathogenic	*Melampsora laricis-populina*	http://genome.jgi.doe.gov/Mellp1/Mellp1.home.html	10
	Puccinia graminis	http://genome.jgi-psf.org/Pucgr1/Pucgr1.home.html	10
	Ustilago maydis	http://www.broad.mit.edu/annotation/genome/ustilago_maydis/Home.html, http://mips.gsf.de/genre/proj/ustilago/	8
Parasitic	*Tremella mesenterica*	http://genome.jgi-psf.org/Treme1/Treme1.home.html	11
Ectomycorrhiza	*Laccaria bicolor*	http://genome.jgi-psf.org/Lacbi2/Lacbi2.home.html, http://mycor.nancy.inra.fr/IMGC/LaccariaGenome/	7
	Piriformospora indica	http://genome.jgi-psf.org/Pirin1/Pirin1.home.html	77
Yeast	*Cryptococcus neoformans* var. *grubii*	http://genome.jgi.doe.gov/Cryne_H99_1/Cryne_H99_1.home.html	81
	Rhodotorula glutinis	http://www.ncbi.nlm.nih.gov/nuccore/AEVR00000000	82
Mold-like	*Wallemia sebi*	http://genome.jgi.doe.gov/Walse1/Walse1.home.html	207

tively) (Table 4), which encode other putative cellulolytic enzymes, such as BGLs and EGs, occur in all white rot fungi. White rot fungi also possess a large set of genes encoding putative hemicellulose- and pectin-active enzymes from various CAZyme families. On average, they have more copies of genes from GH families 10 and 11 (xylan related), 28 (pectin related), 43 (xylan and pectin related), and 74 (xyloglucan related) and carbohydrate esterase (CE) families 1 (xylan related) and 12 (pectin related) than other

TABLE 4 Distribution of CAZyme-encoding genes in basidiomycetes and *Aspergillus* species[d]

Ecology	White rot																Brown rot								Litter-/Straw-decomposing/ Coprophilic				Plant pathogen/ Parasitic				ECM		Yeast/ Mold		*Aspergillus* species			
Species	*A. subglabra*	*B. adusta*	*C. subvermispora*	*D. squalens*	*F. mediterranea*	*G. lucidum*	*Ganoderma* sp.	*H. irregulare*	*P. carnosa*	*P. chrysosporium*	*P. brevispora*	*P. ostreatus*	*P. strigosozonata*	*S. hirsutum*	*T. versicolor*	*S. commune*†	*B. botryosum**	*J. argillacea**	*C. puteana*	*Dacryopinax* sp.	*F. pinicola*	*G. trabeum*	*P. placenta*	*S. lacrymans* 7.9	*W. cocos*	*A. bisporus* var. *bisporus*	*G. marginata*	*V. volvacea*	*C. cinerea*	*M. laricis-populina*	*P. graminis*	*U. maydis*	*T. mesenterica*	*L. bicolor*	*P. indica*	*C. neoformans* var. *grubii*	*R. glutinis*	*W. sebi*	*A. fumigatus*	*A. nidulans*	*A. niger* (ATCC1015)	*A. oryzae*
CAZy family																																									
GH1	1	-	3	4	5	3	3	2	2	2	-	3	1	3	2	3	4	3	3	1	2	5	2	3	1	1	5	3	2	0	0	0	1	0	1	0	-	1	5	3	3	3
GH2	7	-	4	4	2	3	3	3	2	2	-	3	4	3	5	4	2	3	5	3	4	4	3	3	3	2	3	2	2	4	10	1	1	2	2	0	-	2	6	10	6	7
GH3	$12^a/_{14}$	9	6	$7^a/_8$	$7^a/_8$	12	13	$11^a/_{12}$	11	$9^a/_{11}$	8	13	$12^a/_{14}$	$15^a/_{17}$	$11^a/_{13}$	12	7	10	$12^a/_{13}$	$8^a/_9$	12	$9^a/_{11}$	6	$9^a/_{10}$	8	8	11	11	7	$3^a/_3$	2	3	$3^a/_3$	2	8	7	-	4	18	20	19	23
GH5	$8^b/_{43}$	19	18	$5^b/_{19}$	$6^b/_{20}$	19	18	$7^b/_{16}$	24	$5^b/_{19}$	23	21	$6^b/_{18}$	$6^b/_{20}$	$5^b/_{22}$	16	29	36	$8^b/_{21}$	$5^b/_{24}$	19	$5^b/_{19}$	17	$8^b/_{20}$	18	19	40	17	26	$7^b/_{29}$	27	12	$0^b/_{13}$	$1^b/_{23}$	23	10	-	9	13	15	10	13
GH6	2	1	1	1	2	1	1	1	1	1	1	3	1	1	1	1	3	3	2	0	0	0	0	1	0	1	3	14	5	0	0	0	0	0	2	0	0	0	1	2	2	1
GH7	8	5	3	4	2	3	3	1	5	9	4	16	5	3	4	2	7	5	2	0	0	0	0	0	0	1	8	0	6	8	8	0	0	0	1	0	0	0	4	3	2	3
GH9	0	1	0	0	1	2	1	1	1	1	1	1	1	1	1	1	3	1	1	1	0	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	-	0	0	0	0	0
GH10	4	4	6	5	4	7	9	2	5	6	8	3	5	6	6	5	11	5	3	3	2	3	3	1	4	2	9	19	5	6	5	2	0	0	20	0	0	0	4	3	2	4
GH11	3	0	1	0	0	0	0	0	1	1	0	2	1	1	0	1	0	0	0	0	0	0	0	0	0	2	8	0	6	0	0	1	0	0	16	0	0	0	3	2	3	4
GH12	1	2	2	3	3	3	3	4	3	2	2	2	2	5	5	1	0	8	4	1	2	2	2	2	2	2	4	2	1	10	3	0	0	3	1	0	-	0	4	1	3	4
GH25	1	1	1	2	1	2	2	0	0	1	1	2	1	0	1	1	2	1	2	0	0	2	0	1	0	4	0	-	0	0	0	1	0	0	0	0	-	0	3	3	0	1
GH26	0	-	0	0	0	0	0	0	0	0	-	0	0	0	0	1	1	0	0	4	0	0	0	0	0	0	0	0	0	3	4	1	0	0	1	0		0	0	3	1	1
GH28	14	-	6	7	17	13	10	8	4	4	-	6	13	17	11	3	2	7	13	6	12	10	8	7	9	6	20	3	3	3	1	1	0	7	6	1	1	0	14	9	22	21
GH30	1	1	1	2	2	2	3	2	3	2	2	4	3	5	4	5	3	1	7	4	10	3	3	2	2	3	2	2	3	0	0	2	0	9	1	0	-	0	1	0	1	0
GH35	6	4	1	3	2	10	7	4	4	3	4	4	4	7	2	4	1	2	2	1	2	2	1	3	2	1	10	4	0	1	1	1	0	1	3	0	-	0	5	4	5	7
GH36	0	-	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	-	0	3	4	2	3
GH37	3	3	2	3	3	2	2	2	2	2	3	2	2	2	2	2	2	2	4	2	2	2	3	2	4	2	2	2	2	3	3	2	2	2	2	2	-	2	1	1	1	1
GH43	28	-	2	7	7	11	11	4	4	4	-	8	7	12	3	19	1	3	6	5	7	6	1	2	1	4	6	8	4	8	2	3	0	0	6	0	-	0	18	15	11	20
GH45	2	3	1	2	0	2	3	2	1	2	4	2	1	1	2	1	1	2	1	1	1	1	0	0	0	1	2	0	0	0	0	2	0	0	1	0	-	0	1	1	0	0
GH51	3	-	2	2	1	2	2	1	2	2	-	3	3	3	2	2	1	3	3	2	2	4	1	1	4	1	5	3	1	3	0	2	0	0	0	1	-	0	2	2	4	3
GH53	1	-	6	1	1	1	1	1	1	1	-	1	2	2	1	1	1	2	1	1	1	2	1	1	1	1	3	1	1	0	0	0	0	0	1	0	-	0	1	1	1	1
GH54	0	-	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	8	-	0	0	0	0	0	0	0	0	-	0	1	1	1	1
GH62	0	-	0	0	0	0	0	0	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	-	3	0	0	1	0	0	3	0	-	0	2	2	1	2
GH67	-	-	0	0	0	0	0	0	-	0	-	-	-	-	-	0	-	-	0	-	0	0	0	0	-	0	-	0	-	0	0	0	-	0	-	-	-	-	1	1	1	1
GH74	1	2	1	1	4	1	1	1	2	4	1	3	2	2	1	1	0	1	0	0	0	1	0	1	0	1	2	1	1	0	0	0	0	0	1	0	-	0	2	2	1	0
GH78	4	-	1	5	2	5	3	2	1	1	-	2	7	3	3	3	0	1	2	0	3	2	3	2	3	4	2	0	0	0	0	0	0	0	0	3	-	0	6	8	8	9
GH93	1	-	0	1	0	2	1	0	0	0	-	0	1	1	0	2	0	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	-	0	3	2	1	3
GH115	2	-	2	2	3	4	4	1	1	1	-	1	1	2	2	2	1	2	2	2	1	2	1	1	2	2	1	3	1	0	0	1	0	0	1	1	-	0	1	1	0	4
CE1	4	2	2	0	0	3	2	1	2	4	2	2	2	1	3	11	2	2	0	0	0	1	0	0	0	1	2	5	4	0	0	1	0	0	9	1	9	0	5	3	3	5
CE5	3	-	0	0	0	0	1	0	-	0	-	0	1	1	0	1	0	0	1	0	0	0	0	0	0	6	6	1	6	12	0	3	0	1	3	0	-	1	5	4	5	5
CE8	2	-	2	3	3	3	3	3	2	2	-	2	6	5	2	2	2	2	2	3	2	2	2	2	1	2	3	3	0	4	7[c]	1	0	4	5	0	-	0	6	3	3	5
CE12	2	-	0	2	2	1	1	2	-	0	-	2	1	3	0	2	1	0	0	0	0	0	0	0	0	2	4	1	1	0	-	0	0	0	1	0	-	0	3	2	2	4
CE15	6	2	2	2	1	2	2	1	3	3	2	1	2	1	2	2	3	0	0	1	1	1	1	0	1	1	1	-	15	0	-	0	0	0	1	0	-	0	1	0	0	0
CE16	12	-	5	13	6	17	17	6	5	1	-	9	12	14	8	11	7	8	7	3	8	7	4	4	6	11	10	6	2	1	1[c]	0	1	4	7	0	-	0	3	3	3	3
PL1	2	-	0	0	2	0	0	2	0	0	-	10	4	4	0	5	4	0	0	0	0	0	0	0	0	2	2	11	1	4	4	1	0	0	3	0	-	0	6	8	7	12
PL3	1	-	0	0	0	0	0	0	0	0	-	3	0	0	0	4	2	0	0	0	0	0	0	0	0	1	0	-	2	0	0	0	0	0	6	0	-	0	3	5	0	3
PL4	1	-	0	1	0	0	0	1	0	0	-	2	3	3	1	3	1	0	0	0	0	2	0	0	0	1	0	2	2	0	0	0	0	0	2	1	-	0	3	4	2	4
PL9	0	-	0	0	0	0	0	0	0	0	-	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	1	0	-	0	1	1	0	1
PL11	-	-	0	0	0	0	0	0	-	0	-	-	-	-	-	0	-	-	0	-	0	0	0	0	-	0	-	-	-	0	0	0	-	0	-	-	-	-	0	1	0	0
AA3_1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	2	0	0	1	0	2	0	1	1	-	1	0	0	0	0	0	2	0	-	0	2	2	2	2
AA9	20	28	9	15	13	15	16	10	11	15	12	29	14	16	18	22	32	15	10	0	4	4	2	5	2	11	19	30	33	4	3	0	0	13	25	1	-	10	7	9	8	8

[a] No β-*N*-acetylhexosaminidase was included.
[b] β-1,4-Endoglucanase and β-1,4-endomannanase are included.
[c] Can also include models associated with more than one category.
[d] Gene numbers are based on previously reported data for the following organisms, and basidiomycete data are updated according to Riley et al. (55): *Agaricus bisporus* var. *bisporus* (9), *Aspergillus fumigatus* (208), *Aspergillus nidulans* (49, 209), *Aspergillus niger* (ATCC 1015) (84, 210), *Aspergillus oryzae* (211), *Auricularia subglabra* (11), *Bjerkandera adusta* (205), *Botryobasidium botryosum* (55), *Ceriporiopsis subvermispora* (12), *Coniophora puteana* (11), *Coprinopsis cinerea* (206), *Cryptococcus neoformans* var. *grubii* (81), *Dacryopinax* sp. (11), *Dichomitus squalens* (11), *Fomitiporia mediterranea* (11), *Fomitopsis pinicola* (11), *Galerina marginata* (55), *Ganoderma lucidum* (14), *Ganoderma* sp. (205), *Gloeophyllum trabeum* (11), *Heterobasidion irregulare* (66), *Jaapia argillacea* (55), *Laccaria bicolor* (7), *Melampsora laricis-populina* (10), *Phanerochaete carnosa* (45), *Phanerochaete chrysosporium* (6), *Phlebia brevispora* (205), *Piriformospora indica* (77), *Pleurotus ostreatus* (55), *Postia placenta* (18), *Puccinia graminis* (10), *Punctularia strigosozonata* (11), *Rhodotorula glutinis* (82), *Schizophyllum commune* (15), *Serpula lacrymans* 7.9 (71), *Stereum hirsutum* (11), *Trametes versicolor* (11), *Tremella mesenterica* (11), *Ustilago maydis* (8), *Wallemia sebi* (207), *Wolfiporia cocos* (11), and *Volvariella volvacea* (13). †, white rot-like; *, ecological classification uncertain; —, not in published papers.

wood-rotting and litter-decomposing basidiomycetes (Table 4). Genes belonging to polysaccharide lyase (PL) families PL3, -9, and -11 are almost absent, while some species have few representatives in PL1 and -4. Notably, high numbers of gene copies in PL1 were annotated for *P. ostreatus* (Table 4). For the oxidoreductases involved in plant polysaccharide degradation, white rot fungi possess typically 1 copy of a CDH (families AA3_1 and AA8)-encoding gene and up to 29 copies of LPMO (AA9)-encoding genes. In this respect, *J. argillacea* resembles white rot fungi, as it harbors similar numbers of genes encoding CDH and LPMOs (Table 4). Interestingly, *B. botryosum* has more genes encoding CDHs and LPMOs than any white rot fungus sequenced so far (55).

The first basidiomycete genome sequenced is the model white rot fungus *P. chrysosporium* (6, 57). Its CAZyme content shows many similarities to the genomes of other white rot basidiomycetes by carrying, for instance, several genes that encode putative cellulose-hydrolyzing enzymes (EGs, CBHs, and BGLs) (Table 4), which enables it to completely degrade cellulose (6). *P. chrysosporium* secretes CBHI, CBHII, EGs, and BGL when grown on microcrystalline cellulose (Avicel) (58). As these cellulases were not found in *P. chrysosporium* under ligninolytic culture conditions, they do not seem to be constitutively produced (57). In Avicel cultures of *P. chrysosporium*, the expression of oxidatively polysaccharide-degrading CDH- and putative LPMO-encoding genes was detected together with the expression of genes encoding classical cellulases (17). *P. chrysosporium* is also able to degrade hardwood hemicelluloses into their building blocks (6). Genes encoding hemicellulolytic and pectinolytic enzymes (e.g., GH10 xylanase, a putative GH28 exopolygalacturonase, and a putative CE1 acetyl xylan esterase) were expressed, and the corresponding proteins were secreted in both Avicel and carbon-limited liquid cultures, suggesting constitutive expression of the corresponding genes (17, 57, 58).

Only a limited number of pectinolytic genes are present in the genome of *P. chrysosporium*. For example, pectin/pectate lyase-, exoarabinanase-, or rhamnogalacturonan hydrolase-encoding genes were not detected (6). Despite this low pectinolytic potential, *P. chrysosporium* is able to grow on solid cultures of pectin substrates with a high degree of methyl esterification, such as soy, apple, and lemon pectins, possibly producing endopolygalacturonase together with galactan- and arabinan-hydrolyzing 1,4-β-endogalactanase (GH53), β-galactosidase (GH35), and α-arabinofuranosidase (GH51) (44). However, poor growth on rhamnogalacturonan and polygalacturonic acid was observed (44).

Several studies comparing the plant-polysaccharide-degrading ability of *P. chrysosporium* to those of other basidiomycetes have been conducted. The selective white rot fungus *Ceriporiopsis* (*Gelatoporia*) *subvermispora*, which depolymerizes mainly lignin and hemicelluloses and leaves cellulose almost intact, has a GH family distribution similar to that of *P. chrysosporium*. However, some key differences between these fungi can be pointed out. *C. subvermispora* possesses fewer GH3 (including BGL)-encoding genes, with only six copies in the genome (12), while *P. chrysosporium* and the other sequenced white rot species harbor at least 8 genes (Table 4). Also, modest transcript levels for the genes from GH5, -6, -7, and -12 were observed during the growth of *C. subvermispora* on semisolid aspen wood cultures compared to those observed during the growth of *P. chrysosporium*, suggesting a significant reduction in the expression levels of putative cellulase-encoding genes by the selective white rot fungus. This shortage and low-level expression of cellulase genes are compensated by a greater dependence on oxidoreductases, which is in line with the growth pattern of *C. subvermispora* showing preference for lignin depolymerization (12). *C. subvermispora* grows better on pectin and guar gum (galactomannan) than on cellulose (12). In fact, *C. subvermispora* has more endopolygalacturonase (GH28)-encoding genes (six) than *P. chrysosporium* (four), but significant differences in the amounts of other pectinolytic genes between these two white rot species were not detected.

Phanerochaete carnosa, a member of the same genus as *P. chrysosporium*, is found on softwoods, while most other studied white rot fungi are typically isolated from hardwood (45). The chemical compositions of the cell walls of softwoods and hardwoods differ particularly in their hemicelluloses structures (mainly galactoglucomannans are present in softwood, while glucuronoxylan is the most abundant hemicellulose in hardwood) and in the slightly higher lignin contents of softwoods (20). The genome of *P. carnosa* contains 193 GH gene models, which is higher than the number of gene models in the genome of *P. chrysosporium* (182 gene models) (45). When the secretome of *P. carnosa* grown in cellulose and spruce wood cultures was analyzed, the fungus produced a pattern of classical cellulases (GH3 EGs and BGLs and GH6 and -7 CBHs), xylanases (GH10 and -11), debranching hydrolases (GH43), and glucuronoyl esterases (CE1) together with putative LPMOs (AA9) that was similar to the pattern produced by *P. chrysosporium* (59). Interestingly, a GH2 β-mannosidase, which was not detected by proteomic analyses in cellulose or wood cultures of *P. chrysosporium* (17, 57), was present in cellulose-containing cultures of *P. carnosa* (59). Also, peptides corresponding to a GH5 mannanase were identified in cellulose cultures of *P. carnosa*. In addition, *P. carnosa* grows better (based on radial growth and mycelium density) on guar gum (galactomannan) than on xylan- and pectin-containing substrates (45), thus supporting its preference for softwood bioconversion. Biochemical characterization of *P. carnosa* hemicellulases is still needed to confirm a correlation between growth profiles and enzyme substrate specificities.

Another white rot fungus isolated mainly from softwood, e.g., western yellow pine (*Pinus ponderosa*) and old coniferous trunks (60), *Dichomitus squalens*, has a CAZyme repertoire typical of white rot species (11). It is able to grow on cellulose-, pectin-, and lignin-containing minimal media, and it shows better growth on galactomannan than on xylan. Together with *Fomitiporia mediterranea*, it lacks the CE1 genes encoding putative xylan- and pectin-debranching enzymes. *D. squalens* also shows a decreased ability to grow on pectin than on D-glucose, which is in contrast to the majority of the species studied so far (11). A recent study shows that the genes encoding CBHs, LPMOs, and CDH are coexpressed when *D. squalens* grows on spruce wood and in microcrystalline cellulose (Avicel)-containing cultures. Moreover, the simultaneous expression of the *cdh* and *lpmo* genes emphasizes the role of oxidative degradation of cellulose together with hydrolytic cellulases in white rot fungi (61).

Ganoderma lucidum is a wood-decaying white rot species and a model medicinal fungus traditionally used in Asia. It produces a large variety of bioactive compounds, thus harboring potential for medical applications (14). *G. lucidum* possesses a relatively large number of genes encoding putative CAZymes, including 288 GHs, compared to other white rot basidiomycetes with all the major cellulose-, hemicellulose-, and pectin-degrading genes (14,

62). Similar to most white rot fungi, its genome lacks the genes for putative pectin lyase, pectate lyase, and rhamnogalacturonan lyase (PL1, -3, -9, and -11) (14).

Based on morphological features, *Auricularia subglabra* belongs to a group of so-called jelly fungi. *A. subglabra* is found on dead and decaying wood, where it causes white rot (11). Compared to the genomes of other white rot species, the genome of *A. subglabra* (formerly deposited as *Auricularia delicata* in the JGI database) harbors a large number of GH43 and CE16 genes, which include putative β-1,4-xylosidase-, endoarabinanase-, α-L-arabinofuranosidase-, and acetylesterase-encoding activities. Cross sections of colonized wood demonstrate the ability of *A. subglabra* to extensively degrade all the main polymers of the wood cell wall (11). However, it lacks specific xylan side-chain-hydrolyzing enzymes, such as arabinoxylan arabinofuranohydrolases (11).

Schizophyllum commune is a model basidiomycete for mushroom development (15). It has been classified as a white rot fungus, although it has a limited lignin-degrading capacity and therefore does not correspond to the typical characteristics of white rot species. Instead, *S. commune* has one of the most extensive cellulose- and hemicellulose-degrading enzyme sets, and each fungal CAZyme family related to plant biomass degradation is represented in its genome (Table 4) (15). *S. commune* is found mainly on fallen hardwood, but it also colonizes softwood and grass silage. *S. commune* is rich in GH43 enzyme-encoding genes, which include β-1,4-xylosidase and endoarabinanase, and genes encoding xylan- and pectin-degrading enzymes. Another uncommon characteristic of *S. commune* is the wealth of putative pectin-degrading lyases (PL1, -2, and -4), which correlates with high-level pectinase production (15, 63). This is consistent with the strategy of *S. commune* to invade adjacent parenchymatic cells in plant xylem tissue through pectin-surrounded simple and bordered pits (15).

The dual life-style of the necrotrophic white rot fungus and economically important forest pathogen *Heterobasidion irregulare* (formerly known as *H. annosum*, intersterility group P [64]) involves pathogenic and saprobic life-styles, which are reflected in its genome and transcriptome (65). Similar to saprobes, it has all the enzymes for digesting cellulose/xyloglucan (GH5, -6, -7, -12, -27, -29, -45, and -74) and pectin (GH28, -43, -51, -53, -78, and -105; PL1 and -4; and CE8 and -12). However, the whole CAZyme arsenal is used only during the saprobic growth phase of *H. irregulare*, while fewer CAZyme-encoding genes are expressed during the pathogenic phase (66). This shows that *H. irregulare* has the ability to extensively degrade plant material, but the fungus uses its full CAZyme repertoire only when it becomes less dependent on its living host (66). Other plant-pathogenic basidiomycetes are discussed in "Plant-Pathogenic Fungi and Mycoparasites," below.

Brown rot fungi. Brown rot fungi represent ~6 to 7% of the known wood-rotting basidiomycetes and occur mostly on conifers (gymnosperms), which are softwoods (53). While brown rot fungi are able to efficiently and rapidly break down wood cellulose and hemicelluloses, they only modify lignin, mainly by demethoxylation, resulting in a characteristic brown residue of decayed wood (56). In contrast to the enzymatic approach of white rot fungi (6, 67), brown rot fungi initiate cellulose breakdown with highly reactive oxidants, such as low-molecular-weight free radicals, including the hydroxyl radicals formed through the Fenton reaction (68, 69). The difference in cellulose-depolymerizing abilities between white and brown rot fungi is probably a result of multiple evolutionary steps that have led to these two different life-styles (11). This can be seen, for example, by the loss of lignin-modifying peroxidases, which has been proposed to have occurred several times, resulting in the divergence of brown rot fungi in the orders Polyporales (e.g., *Fomitopsis pinicola*, *Postia placenta*, and the plant-parasitic brown rot fungus *Wolfiporia cocos*) and Boletales (e.g., *Coniophora puteana* and *Serpula lacrymans*) and species *Gloeophyllum trabeum* and *Dacryopinax* sp. (11).

A comparison of the representatives of the different CAZyme families in each plant-biomass-modifying basidiomycete group indicates that the brown rot fungi studied up to now possess a significantly smaller set of plant-polysaccharide-depolymerizing enzymes than white rot and litter-decomposing fungi (Table 4). The most obvious reduction in the CAZymes of brown rot fungi can be seen in the small number of putative CBHs (GH6 and -7) (18, 70). Only the species of the order Boletales and closely related to ECM fungi, *S. lacrymans* and *C. puteana*, harbor one and four putative CBH-encoding genes, respectively. Also, the genome of *Postia placenta* lacks genes for CBHs and for carbohydrate binding modules from family 1 (CBM1) and contains only two putative β-1,4-endoglucanase-encoding genes (18). Although the genomes of brown rot fungi contain fewer genes encoding CDHs (AA3_1 and AA8) and LPMOs (AA9) than those of white rot fungi, it is possible that these putative oxidoreductases of brown rot fungi take part in enzymatic cellulose depolymerization (11, 18, 71). However, considering the overall lower number of LPMOs and greater variety in the absence and presence of CDH in brown rot fungi, this implies that their ability to utilize oxidized sugars is also more variable than in white rot fungi. When secretomes from semisolid aspen cultures of brown rot fungi were analyzed, only *C. puteana* and *G. trabeum* secreted a putative CDH and LPMO, respectively, while none of these proteins were detected in *F. pinicola* or *W. cocos* (11).

The substrate preference of brown rot basidiomycetes for softwoods can also be explained by the characteristics of their hemicellulose-degrading capacity. While hardwoods are known to have a higher proportion of xylan, softwoods have a higher mannan content. During the evolution of the brown rot fungal life-style, the number of genes encoding enzymes assigned to GH10 and -11 (endoxylanases) and CE15 was reduced (18, 70). Therefore, brown rot fungi have slightly lower numbers of xylanolytic enzymes than white rot fungi. In addition, the genomes of *C. puteana*, *Dacryopinax* sp., *F. pinicola*, *P. placenta*, and *S. lacrymans* lack genes encoding putative acetyl xylan or feruloyl esterases from CE1. Instead, brown rot fungi grow well on guar gum, which is a galactomannan similar in structure to softwood cell wall galactomannans (11). Several copies of genes encoding putative β-1,4-endomannanases involved in the degradation of mannan are present in the genomes of brown rot basidiomycetes, presumably helping them to colonize softwoods.

Litter- and Straw-Decomposing Fungi

Litter- and straw-decomposing basidiomycetes participate significantly in the Earth's carbon cycle, together with wood-decaying fungi. The genomes of the litter-decomposing fungus *Agaricus bisporus* and the straw-decomposing species *Volvariella volvacea* (Table 3) have been sequenced because of their importance as cultivated mushrooms and in recycling decaying plant matter. The genomes of two *A. bisporus* strains show similar gene contents with respect to plant polysaccharide degradation. The economi-

cally important white button mushroom *A. bisporus* var. *bisporus* originates from Europe, while *A. bisporus* var. *burnettii* grows on leaf litter in North America (9). Another edible fungus, *V. volvacea*, is widely cultivated in Asia, where it is grown on rice straw, cotton waste, and other agricultural by-products (13). In addition, the genome of another litter-decomposing species, *Galerina marginata*, was recently reported (55).

A. bisporus, *G. marginata*, and *V. volvacea* have a close evolutionary relationship with white rot basidiomycetes and ECM fungi (9, 55, 72), although their genome content resembles that of white rot rather than ECM genomes. All these fungi grow on partially decayed plant matter, have diverse sets of CAZymes, and are able to cause white rot (Table 4). Although litter- and straw-decomposing fungi and the ECM fungi are taxonomically closely related, their dissimilar ecological niches have resulted in different CAZyme repertoires (Table 4). Generally, saprobes are more capable of degrading plant polysaccharides than root symbionts. For example, the coprophilic fungus *Coprinopsis cinerea* and the litter decomposer *G. marginata* secrete a broader set of plant cell wall-degrading enzymes than the ECM fungus *Amanita bisporigera* (73).

Nonwoody plant tissues contain relatively large amounts of pectin (74). In accordance with this, some forest litter-decomposing basidiomycetes have been shown to produce pectinolytic enzymes (75). *A. bisporus* and *G. marginata* harbor two putative pectinolytic enzymes encoding genes from PL1, whereas *V. volvacea* possesses 11 PL1-encoding genes. Up to 5 CE1, 6 CE5, 3 CE8, 4 CE12, and 11 CE16 genes encoding putative carbohydrate esterases have been found in the genomes of these litter- and straw-decomposing fungi, while the CE1, -5, and -12 genes are missing from several white and brown rot fungal species (Table 4). While *A. bisporus*, *G. marginata*, and *V. volvacea* have a wide spectrum of CE genes, only one gene encoding a putative 4-*O*-methyl-glucuronoyl methyl esterase (CE15) has been detected in *A. bisporus* and *G. marginata*.

Ectomycorrhizal Fungi

Mycorrhizal fungi depend largely on their plant symbionts for their carbon source (76), and thus, they have a less extensive CAZyme arsenal than the wood-rotting and litter- and straw-decomposing fungi (7, 9, 72, 73). The limited plant-polysaccharide-degrading capability of ECM fungi is a result of evolutionary reduction in CAZyme families (7, 71) to suit their role as root symbionts. The few CAZymes of ECM fungi are most probably needed for the modification of cell walls of plant roots in order to establish contact with their host for nutrient exchange. This is supported by the tightly controlled expression of putative CAZyme-encoding genes of *Piriformospora indica* during the fungal colonization of living plant roots (77). Five LPMO-encoding genes are upregulated at the prepenetration stage, while GH10-, GH11-, GH18-, and GH62-encoding genes are induced during prepenetration, colonization, and postcolonization, thus suggesting a role of GHs in the local secretion of enzymes at the penetration site (77). The reduction in CAZymes is also observed for the genome of *L. bicolor* and *Paxillus involutus* (7, 78). *L. bicolor* possesses mostly enzymes that modify polysaccharide backbones, such as β-1,4-endoglucanase, polygalacturonases, and β-1,4-endomannanses for cellulose, pectin, and galactomannan degradation, respectively, but the number of putative genes encoding accessory enzymes is limited. The most abundant CAZyme family acting on the plant cell wall in the genome of *L. bicolor* is LPMO (7). *P. involutus* has a unique enzymatic system, similar to that of brown rot fungi, to decompose plant biomass (78, 79). Transcriptomic studies of *P. involutus* have revealed that only one β-1,4-endoglucanase (GH9) and two LPMO genes are expressed during growth on plant litter or cellulose (79). The oxidative depolymerization of cellulose in cooperation with CDH or low-molecular-weight reducing agents (28, 31) supports the role of LPMOs as important components of the radical-based cellulose-degrading mechanism of ECM fungi. We suggest that most CAZyme activities have been lost in ectomycorrhizal fungi as an adaptation to symbiotic growth on host photosynthate. The CAZyme arsenal of some ECM basidiomycetes, such as *P. indica*, reflects their ability to switch their life-styles from mutualist to saprobe. *P. indica* associates with living and dead barley roots and a variety of mono- and dicotyledonous plants. When exposed to dead plant matter instead of living plant roots, *P. indica* upregulates several of its pectin-related enzymes, thus indicating a switch from a mutualistic to a saprobic life-style (77).

Plant-Pathogenic Fungi and Mycoparasites

Ustilago maydis, *Melampsora laricis-populina*, and *Puccinia graminis* are obligate biotrophic pathogens that derive nutrients from living plant tissues and are not able to survive without their hosts. In contrast to the genomes of more aggressive ascomycete pathogens such as *Magnaporthe grisea* and *Fusarium graminearum*, these basidiomycete pathogens have few genes encoding CAZymes that are most likely employed for penetrating the cell surface of the host plant (8, 10, 11, 66). The limited CAZyme set also reflects the avoidance of extensive damage of the host cell walls, which can trigger the immune response of the plant (8). However, the GH5 (including β-1,4-endoglucanase and β-1,4-endomannanase activity)-encoding genes are present in several copies (up to 29) (Table 4), and they are suggested to modify the polysaccharide backbones of cellulose and hemicelluloses in order to loosen the plant cell wall structure and to further facilitate the entry of fungal hyphae into the host cell. In *M. laricis-populina*-infected cultures of wheat and barley, cellulose- and hemicellulose-depolymerizing CAZyme-encoding genes were highly upregulated (10). A similar upregulation was detected in poplar cultures infected with *P. graminis* (80). This suggests that invading hyphae of these rust fungi secrete polysaccharide-degrading enzymes to form haustoria on the plant surface (10). However, it is possible that these obligate biotrophic pathogens possess as-yet-unidentified strategies for virulence, such as the unexpected set of small genes with unknown function detected in the genome of the corn smut fungus *U. maydis* (8).

Tremella mesenterica is a wood-degrading fungus and mycoparasite of *Peniophora* species that is morphologically classified into the group of jelly fungi. The genome of *T. mesenterica* has a limited CAZyme repertoire similar to that of ECM fungi, containing only three genes encoding GH3 (no β-*N*-acetylhexosaminidase included) and no genes encoding GH families 6, 7, 10, 11, 12, 28, 43, and 74 (11). This may reflect the parasitic life-style of *T. mesenterica*. However, *T. mesenterica* and related species might have an alternative mechanism to degrade plant biomass, but these species have so far been only scarcely studied.

Basidiomycete Yeasts

So far, the genomes of only a few basidiomycete yeast species have been sequenced and analyzed for CAZymes. These unicellular basidiomycetes usually have a very limited pattern of polysaccharide-degrading enzymes, which has been shown for the genomes of *Cryptococcus neoformans* (81) and *Rhodotorula glutinis* (82). Similarly, *Wallemia sebi*, a xerophilic mold-like basidiomycete, has reduced CAZyme sets (55).

Comparison of the Genomes of Basidiomycetes and *Aspergillus* as a Representative of the Plant-Biomass-Degrading Ascomycetes

Aspergillus species are widely studied due to their relevance to human health and economic importance. These species include the industrial workhorses *A. niger* and *A. oryzae* as well as the opportunistic human pathogen *A. fumigatus* (83). Therefore, their genomes were also among the first sequenced fungal genomes. The genomes of aspergilli revealed that these species contain unexpectedly abundant sets of plant-biomass-degrading genes compared to the previously identified genes and enzymes (19, 84). This demonstrated that without genome sequence data, predominantly only the genes and enzymes that are highly expressed and produced under laboratory conditions have been characterized.

A study of six *Aspergillus* species (*A. clavatus*, *A. flavus*, *A. fumigatus*, *A. niger*, *A. oryzae*, and *Neosartorya fischeri* [teleomorph of *A. fischerianus*]) demonstrated that the genome content and organization of closely related species are very similar (85). However, differences in the contents of plant-polysaccharide-degrading genes of *A. nidulans*, *A. niger*, and *A. oryzae* have been detected. *A. oryzae* has a significantly higher number of xylan- and pectin-related genes than the other two species. Instead, *A. nidulans* harbors more galactomannan-related genes than *A. niger* and *A. oryzae*, whereas the number of inulin-related genes is highest in *A. niger* (49). While the aspergilli do not provide representative numbers of genes in CAZyme families for all ascomycete fungi, their generalistic life-style and ability to degrade every plant polysaccharide (49) make them suitable baselines to use for comparisons with other fungi.

Genes related to cellulose degradation. The overall CAZyme contents of the genomes of basidiomycetes and *Aspergillus* species are similar. They both possess several genes encoding GH5 and -12 EGs. Aspergilli and basidiomycetes have similar numbers of genes encoding CBHs (GH6 and -7). However, aspergilli have notably more BGL genes in GH3 than do the basidiomycetes (Table 4). Interestingly, basidiomycetes harbor genes from GH9, while aspergilli lack the GH9-encoding genes (Table 4). LPMO-encoding genes are present in most of the basidiomycete and aspergillus genomes (86), but basidiomycetes have more LPMO gene models (up to 33) than do the *Aspergillus* species (7 to 9) (Table 4). Some ascomycetes have similarly high numbers of LPMOs, e.g., 33 in *Podospora anserina* (50).

Genes related to hemicellulose degradation. Generally, aspergilli have more genes in the CAZyme families encoding putative GH11, GH62, and CE5 enzymes than do wood-decaying white rot and brown rot basidiomycetes (Table 4). GH11 xylanases are absent from the genomes of brown rot fungi (Table 4). GH11 endoxylanases require a different number of nonsubstituted xylose residues to be able to cleave xylan than GH10 xylanases (87), which are present in all basidiomycetes (Table 4). This indicates that the xylan oligosaccharide profile originating from the action of brown rot xylanases will be different from that originating from white rot fungi and *Aspergillus*, which will affect the overall process of xylan degradation by these fungi. Basidiomycete genomes almost universally lack the genes encoding GH62 enzymes (Table 4). There are representatives of GH67 and GH93 genes in the genomes of *Aspergillus* species, while they are almost missing from basidiomycete genomes. In contrast, genes encoding GH30 enzymes, e.g., β-1,4-exoxylanases, are widely present in basidiomycetes and absent from *Aspergillus* species. Basidiomycetes have more genes in CE15 and -16 than do aspergilli.

Genes related to pectin degradation. While pectin is a minor component of wood, both basidiomycetes and *Aspergillus* species possess wide and variable sets of genes encoding pectin-degrading enzymes. Basidiomycetes and aspergilli have up to 20 and 22 genes, respectively, encoding putative GH28 polygalacturonases and rhamnogalacturonases (Table 4). All the brown rot fungi and the white rot species *C. subvermispora*, *P. chrysosporium*, and *Trametes versicolor* lack CE12 genes, which encode putative rhamnogalacturonan acetyl esterases.

CHARACTERIZED PLANT CELL WALL POLYSACCHARIDE-DEGRADING ENZYMES IN BASIDIOMYCETES AND *ASPERGILLUS*

Before the era of genome sequencing, various plant cell wall polysaccharide-degrading enzymes from basidiomycetes were isolated and characterized at the gene or protein level. Several basidiomycete CAZymes have unique biochemical properties, ranging from extreme temperature tolerance and pH to bifunctional catalytic activities. Most of the characterized CAZymes are from the white rot and litter- or straw-decomposing fungi (Tables 5 to 12). These fungi have more copies of putative CAZyme-encoding genes than any other group of basidiomycetes (Table 4). The extensive plant-polysaccharide-degrading ability of white rot fungi stems from their ecology as the dominant wood-degrading species (56).

Cellulose-Degrading Enzymes

Cellulose, the most abundant plant polymer, is hydrolyzed by the extensive set of cellulolytic enzymes of basidiomycetes. EGs, CBHs, and BGLs have been isolated from species that represent various ecophysiological groups, but most of them belong to wood-degrading white rot fungi (Fig. 3 and Tables 5 to 7). On average, the molecular masses of basidiomycete EGs and CBHs are 41 kDa and 53 kDa, respectively (Fig. 3A and Tables 5 and 6). BGLs may be extracellular or cell wall associated, and their structure can be monomeric or multimeric (88). This is shown by the high level of variation in their molecular masses, ranging from 36 to 640 kDa (Fig. 3A and Table 7). In general, these cellulases have acidic pI values, with few exceptions, and acidic pH optima (Tables 5 and 6). The average optimum temperature of the characterized basidiomycete cellulases is between 54°C and 58°C (Fig. 3D and Tables 5 to 7).

Generally, white rot fungi produce more isoenzymes for plant polysaccharide degradation than do other basidiomycetes. Isoenzymes of EGs have been isolated from several white rot species and characterized (Table 5). The molecular mass of the EGs from white rot fungi ranges from 18 to 78 kDa, and they have acidic pI values of 4.1 to 5.7. As an exception, EG of the straw-decomposing fungus *V. volvacea* has a neutral isoelectric point of 7.7 and also a

TABLE 5 Characterized basidiomycete β-1,4-endoglucanases and their biochemical properties

Life-style	Species	CAZyme family	Gene	Enzyme[a]	NCBI protein database accession no.[b]	Molecular mass (kDa)	pI	pH_{opt}	T_{opt} (°C)	Reference(s)
White rot	*Cerrena unicolor*					44		4.0		212
	Dichomitus squalens			En I		42	4.8	4.8	55	213
	D. squalens			En II		56	4.3	4.8	55	213
	D. squalens			En III		47	4.1	4.8	55	213
	Ganoderma lucidum					55	4.7			16
	G. lucidum					43	4.7			16
	Irpex lacteus					56		4.0	50	214
	I. lacteus			En-1		16		4.0	50	215
	I. lacteus			E2-A						216
	I. lacteus			E2-B						216
	I. lacteus	GH5		En-1*		38				217
	Phanerochaete chrysosporium	GH5	*cel5A*	EG36	AAU12275	36	5.6–5.7			58, 90
	P. chrysosporium	GH5	*cel5A*	EG38	AAU12275	38	4.9			58, 90
	P. chrysosporium	GH5	*cel5B*	EG44		44	4.3			58, 90
	P. chrysosporium	GH12	*cel12A*	Cel12A	AAU12276	28	5.2			58, 91
	P. chrysosporium	GH45		*Pc*Cel45A		18				92
	Polyporus arcularius			CMCase I		39		4.4–4.6	68	218
	P. arcularius			CMCase II		36		4.4–4.6	68	218
	P. arcularius	GH3	*cel3A*	CMCase IIIa	BAD98315	24		4.9	52	218, 219
	Sporotrichum pulverulentum[c]			T1		32	5.3			220
	S. pulverulentum[c]			T2a		37	4.7			220
	S. pulverulentum[c]			T2b		28	4.4			220
	S. pulverulentum[c]			T3a		38	4.7			220
	S. pulverulentum[c]			T3b		37	4.2			220
	Trametes hirsuta	GH5		*Th*EG		44				221
	T. hirsuta	GH5		rEG*		50		5.0	50	221
	Trametes versicolor					30				222, 223
Brown rot	*Coniophora cerebella*			A		42		4.7		224
	C. cerebella			B		39		4.2		224
	Fomitopsis palustris					40				225
	F. palustris	GH5		EG47		47				105
	F. palustris			EG35		35				105
	F. palustris	GH12	*cel12*							106
	F. palustris	GH12	*eg2*	EGII	BAF49602	24		3.5	55	226
	Gloeophyllum sepiarium (*Lenzites sepiaria*)					85				227
	G. sepiarium			EGS		45	3.8	4.1	59	108
	Gloeophyllum trabeum			EGT		41	3.1	4.2	62	108
	G. trabeum	GH5		Cel5A		42	4.9			103
	G. trabeum	GH12		Cel12A		28				103
	G. trabeum (*Lenzites trabea*)					29		4.4	70	145
	Serpula incrassata			Cel 25		25	<3.6		50	228
	S. incrassata			Cel 49		49	<3.6			228
	S. incrassata			Cel 57		57	<3.6			228
	Piptoporus betulinus			EG1		62	2.6–2.8	3.5	70	109
	Postia placenta					35–40				229
Straw decomposing	*Volvariella volvacea*	GH5	*eg1*	EG1	AAG59832	42	7.7	7.5	55	89, 230
Plant pathogen	*Polyporus schweinitzii*					45		4.0	60	231, 232
	Sclerotium rolfsii			Endo A		52	4.6	4.0	74	233
	S. rolfsii			Endo B		27	4.2	2.3–3.0	50	233
	S. rolfsii			Endo C		78	4.5	4.0	50	233
	Ustilago maydis	GH45	*egl1*	Egl1	AAB36147					93
Yeast	*Rhodotorula glutinis*					40	8.6	4.5	50	234

[a] Asterisks indicate a heterologously produced enzyme.
[b] See http://www.ncbi.nlm.nih.gov/protein.
[c] Anamorph of *P. chrysosporium*.

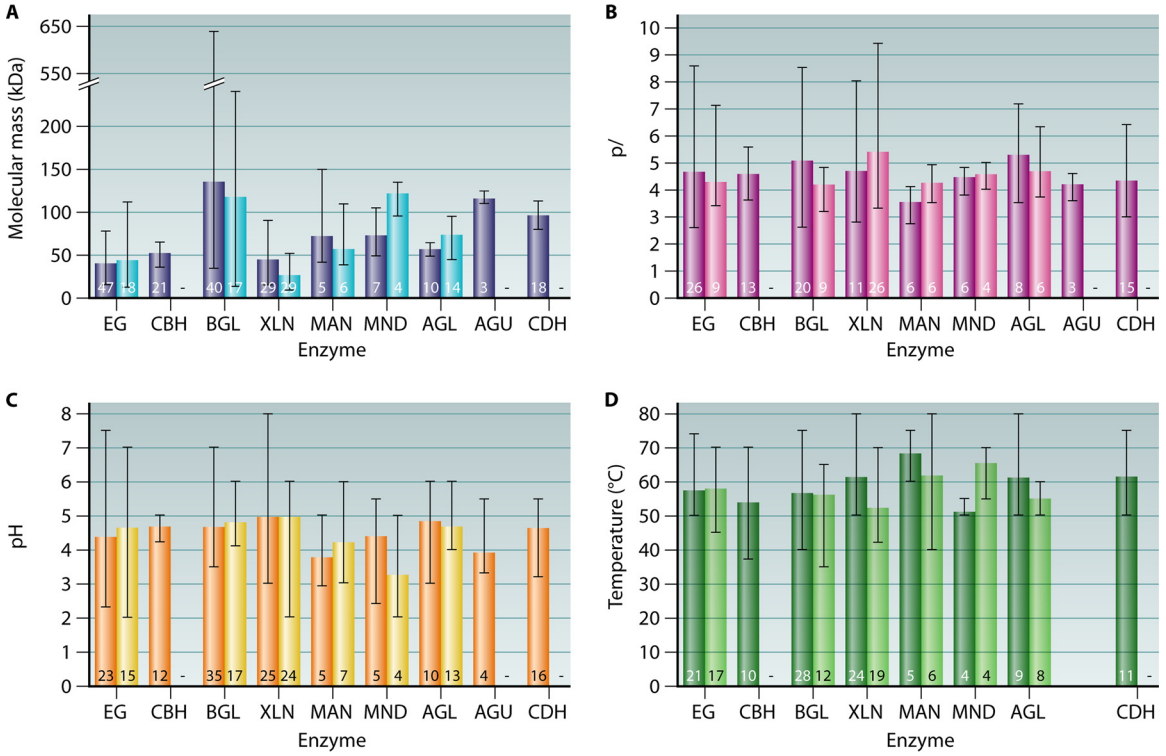

FIG 3 Average molecular masses (kDa for monomers) (A), isoelectric points (pI) (B), pH optima (C), and temperature optima (D) of selected CAZymes from basidiomycetous (first columns, in dark colors) and *Aspergillus* species (second columns, in light colors). EG, endoglucanase; CBH, cellobiohydrolase; BGL, β-glucosidase; XLN, endoxylanase; MAN, endomannanase; MND, β-mannosidase; AGL, α-galactosidase; AGU, α-glucuronidase; CDH, cellobiose dehydrogenase. The number of characterized enzymes used for calculation of mean values is marked at the root of each column. Error bars show the minimum and maximum values reported for each biochemical characteristic. −, no mean value was available.

neutral pH optimum (7.5) for the hydrolysis of carboxymethyl cellulose (CMC) (89). The most comprehensive view of characterized enzymes is from the model white rot fungus *P. chrysosporium*. Three GH5, one GH12, and one GH45 EG of *P. chrysosporium* have been biochemically characterized (58, 90–92). GH5 EGs of *P. chrysosporium* hydrolyze CMC more efficiently than Avicel (90). GH45 EGs have been characterized only for *P. chrysosporium* and the plant pathogen *U. maydis* (92, 93). *P. chrysosporium* GH45 EG hydrolyzes various glycan substrates, preferring substrates consisting mainly of β-1,3/1,4-glucan (92). These endoglucanases show the common synergistic action with CBHs from GH6 and -7 (90, 92).

P. chrysosporium has seven CBH-encoding genes, and three of them have been characterized at the protein level (Table 5). These isoenzymes work synergistically to cleave cellulose at the reducing and nonreducing ends (94). Multiple plant-polymer-degrading isoenzymes produced by one species are hypothesized to have different biochemical properties, such as the substrate specificity to enhance the degradation of plant biomass. The three-dimensional crystal structure of *P. chrysosporium* Cel7D (PDB accession number 1GPI) (95) shows that the catalytic domain is composed of a β-sandwich structure similar to that of ascomycete GH7 CBHI, first solved for the ascomycetous fungus *H. jecorina* Cel7A (PDB accession number 1CEL) (96). The crystal structures reveal that the cellulose binding tunnels of the CBHIs differ significantly, thus affecting the accessibility of the substrate to the active site. In *P. chrysosporium* Cel7D, the cellulose binding tunnel is more open than in *H. irregulare* Cel7A (*Hir*Cel7A) (PDB accession numbers 2YG1 and 2XSP) (97), while *H. jecorina* Cel7A has the most enclosed structure.

Differences in the three-dimensional structures of the six different *P. chrysosporium* CBH proteins were revealed by homology modeling, thus supporting the presence of multiple isoenzymes with different specificities and catalytic mechanisms (95). A function for the multiplicity of cellulolytic-enzyme-encoding genes is also supported by their expression at different phases of fungal growth and degradation of plant biomass. For example, *V. volvacea* has three GH7 CBHI-encoding genes that are expressed during different stages of mushroom development (98).

GH1 and GH3 β-glucosidases of white rot and straw-decomposing fungi have widely variable molecular masses (from 45 to 640 kDa) and isoelectric points (from 3.3 to 8.5) (Table 7). This diversity is due to the intra- and extracellular localizations of β-glucosidases. The exceptions of β-glucosidases with neutral pI values are those from *Fomes fomentarius*, *P. ostreatus*, *P. chrysosporium*, and *V. volvacea* (99–102).

The strategy used by brown rot basidiomycetes to degrade cellulose differs from that used by white rot fungi. Instead of using cellulolytic enzymes, the brown rot fungi rely on highly reactive oxidants for initial depolymerization of plant polysaccharides (18, 56, 71). Most brown rots are unable to degrade crystalline cellulose, with the majority preferring amorphous cellulose (88). However, some brown rot species, e.g., *G. trabeum* and *Fomitopsis palustris*, have been shown to degrade crystalline cellulose

TABLE 6 Characterized basidiomycete cellobiohydrolases and their biochemical properties

Life-style	Species	CAZyme family	Gene	Enzyme	NCBI protein database accession no.[a]	Molecular mass (kDa)	pI	pH_{opt}	T_{opt} (°C)	Reference(s)
White rot	*Dichomitus squalens*			Ex 1		39	4.6	5.0	60	235
	D. squalens			Ex 2		36	4.5	5.0	60	235
	D. squalens	GH7	*cel7b*		CDJ79665					61
	Flammulina velutipes	GH7	*cel7a*	*Fv*Cel7A	BAJ07534	50				236
	F. velutipes	GH7	*cel7b*	*Fv*Cel7B	BAJ07535	60				236
	Ganoderma lucidum					56	5.2			16
	G. lucidum					49	5.0			16
	G. lucidum					50	5.6			16
	Irpex lacteus	GH7	*cel1*	Ex-1	BAA76363	53	4.5	5.0	50	189, 237
	I. lacteus	GH7	*cel2*	Ex-2	BAA76364	56	4.8	5.0	50	189
	I. lacteus	GH7	*cel3*		BAA76365					238
	I. lacteus	GH6	*cex3*		BAG48183	60			50	239
	I. lacteus					65		5.0	50	240
	Lentinula edodes	GH7	*cel7A*	CEL7A	AAK95563					241
	L. edodes	GH6	*cel6B*	CEL6B	AAK95564					241
	Phanerochaete chrysosporium	GH7	*cbh1-1*	Cel7A	CAA38274					95, 192, 242
	P. chrysosporium	GH7	*cbh1-2*	Cel7B	CAA38275					95, 192, 242
	P. chrysosporium	GH7	*cbh1*	Cel7C	AAB46373	62	4.9			94, 95, 192, 242, 243
	P. chrysosporium	GH7	*cbh1-4*	Cel7D	AAA19802	58	3.8			94, 95, 244
	P. chrysosporium	GH7	*cbh1-5*	Cel7E						95
	P. chrysosporium	GH7	*cbh1-6/7*	Cel7F/G						6, 95, 242
	P. chrysosporium	GH6		CBH50		50	4.9			94
	P. chrysosporium	GH6	*cbhII*	CBHII	AAB32942					245
	Polyporus arcularius	GH7	*cel1*		BAF80326					246
	P. arcularius	GH6	*cel2*		BAF80327					246
Brown rot	*Coniophora puteana*			CBHI		52	3.6	5.0		107
	C. puteana			CBHII		50	3.6	5.0		107
	Fomitopsis palustris							4.5	70	104
Litter decomposing	*Agaricus arvensis*	GH7			HM004552[b]	130[c]		4.0	65	247
	Agaricus bisporus	GH6	*cel3AC*	CEL3	AAA50607	52				186
	A. bisporus	GH7	*cel2*		CAA90422					133
Straw decomposing	*Volvariella volvacea*	GH7	*cbhI*	CBHI	AAD41096					98
	V. volvacea	GH6	*cbhII*	CBHII	AAD41097					98
Coprophilic	*Coprinopsis cinerea*	GH6	*CcCel6A*	*Cc*Cel6A	BAH08702					248, 249
	C. cinerea	GH6	*CcCel6B*	*Cc*Cel6B	BAH08703					248, 249
	C. cinerea	GH6	*CcCel6C*	*Cc*Cel6C	BAH08704					248, 249
	C. cinerea	GH6	*CcCel6D*		BAH08705					249
	C. cinerea	GH6	*CcCel6E*		BAH08706					249
White rot plant pathogen	*Heterobasidion irregulare*	GH7		*Hir*Cel7A		50		4.0	45	97
Plant pathogen	*Sclerotium rolfsii*					41.5–42.0	4.3	4.2	37	250
Insect symbiont	*Termitomyces* sp.	GH6		Cellulase I_F		52		4.4		251

[a] See http://www.ncbi.nlm.nih.gov/protein.
[b] Gene identifier.
[c] Dimer.

(103–106). The genomes of brown rot fungi harbor EG- but rarely any CBH-encoding genes, with the exception of the species belonging to the order Boletales, which can also degrade crystalline cellulose (Table 4). GH5 and GH12 EGs from *G. trabeum* and *F. palustris* have also been characterized (Table 5). In microcrystalline cellulose (Avicel) cultures, *G. trabeum* produces GH5 and GH12 EGs, of which GH5 EG was shown to hydrolyze Avicel into cellobiose (103). This processive EG has been suggested to compensate for the lack of CBHs in cellulose degradation of *G. trabeum*. Only *C. puteana* and *S. lacrymans* from the order Boletales

TABLE 7 Characterized basidiomycete β-glucosidases and their biochemical properties

Life-style	Species	CAZyme family	Gene	Enzyme[a]	NCBI protein database accession no.[b]	Molecular mass (kDa)	pI	pH_{opt}	T_{opt} (°C)	Reference(s)
White rot	*Ceriporiopsis* (*Gelatoporia*) *subvermispora*					110		3.5	60	252
	C. subvermispora					53		3.5	60	252
	Fomes fomentarius					58	6.7	4.5–5.0	60	100
	Phanerochaete chrysosporium					90		5.5	45	101
	P. chrysosporium					410		7.0	45	101
	P. chrysosporium					45	4.7	5.0	60	253
	P. chrysosporium					114		4.0–5.2		254
	P. chrysosporium	GH3	*cbgl-1*		AAC26490					255
	P. chrysosporium	GH3	*cbgl-2*		AAC26489					255
	P. chrysosporium	GH3		wtBGL	BAB85988	116				256, 257
	P. chrysosporium	GH3		rBGL*	BAB85988	133				257
	P. chrysosporium	GH1	*bgl1A*	BG1A*	BAE87008	53				113
	P. chrysosporium	GH1	*bgl1B*	BG1B*	BAE87009	60				113
	Pleurotus ostreatus			F1		35	7.5	4.0	40	99
	P. ostreatus			F2		50	7.3	4.0	50	99
	P. ostreatus			F3		66	8.5	5.0	50	99
	Trametes gibbosa					640		3.5	40–50	258
	Trametes versicolor					300		4.3	45	185, 259
	Sporotrichum pulverulentum[c]			A1		165	4.8	4.0–4.5		260
	S. pulverulentum[c]			A2		172	4.5	4.0–4.5		260
	S. pulverulentum[c]			B1-3		165–182	4.6–5.2	4.0–4.5		260
	Stereum hirsutum			BGL		98				261
White rot-like	*Schizophyllum commune*					97		5.3		262
	S. commune			I		102	3.4	5.8		263
	S. commune			II		96	3.3	5.1		263
Brown rot	*Fomitopsis palustris*	GH3	*Cel3A*	Cel3A*	NR	70		5.0	60	146
	Gloeophyllum trabeum (*Lenzites trabea*)					320		4.5	75	145, 264
	Piptoporus betulinus			BG1		36	2.6	4.0	60	109
	Poria vaillantii							4.2	50	265
Litter decomposing	*Agaricus bisporus*		*bg1*		CAC03462					—[d]
Straw decomposing	*Volvariella volvacea*			BGL-I		158	5.6	7.0	55–60	102
	V. volvacea			BGL-II		256	5.0–5.2	6.2	55–60	102
	V. volvacea	GH3	*bgl*		AAG59831	95				266
Plant pathogen	*Sclerotium rolfsii*			BG-1		90	4.1	4.2	68	187
	S. rolfsii			BG-2		90	4.6	4.2	68	187
	S. rolfsii			BG-3		107	5.1	4.2	68	187
	S. rolfsii			BG-4		92	5.6	4.2	68	187
	Ustilago esculenta	GH3		*Ue*Bgl3A*	BAK61808	110		5.0	40	267
Ectomycorrhiza	*Tricholoma matsutake*					160		5.0	60	268
	Pisolithus tinctorius					450[e]	3.8	4.0	65	269
Insect symbiont	*Termitomyces clypeatus*					116		5.0	45	270
	T. clypeatus					110	4.5	5.0	65	271
Yeast	*Rhodotorula minuta*					144	4.8	4.7–5.2	70	188
	Sporobolomyces singularis	GH1	*bglA*	BglA	BAD95570	74		3.5	45	112

[a] Asterisks indicate a heterologously produced enzyme. wtBGL, wild-type BGL.
[b] See http://www.ncbi.nlm.nih.gov/protein. NR, not reported.
[c] Anamorph of *P. chrysosporium*.
[d] Available in the GenBank database (http://www.ncbi.nlm.nih.gov/GenBank/).
[e] Trimer.

possess either one or both GH6 and GH7 CBH gene models (Table 4). The GH6 and GH7 CBHs of *C. puteana* have also been isolated and characterized (Table 6) (107).

Both basidiomycetes and aspergilli have a complete set of hydrolytic cellulases, including EGs, CBHIs, CBHIIs, and BGLs. Only some of the brown rot, plant-pathogenic, and ECM fungi and basidiomycetous yeasts lack CBHs. Similar to the EGs and BGLs from *Aspergillus* species (19), several basidiomycete cellulases are able to degrade the backbone of hemicelluloses (88). EGs from *P. chrysosporium*, *G. trabeum*, *Piptoporus betulinus*, and *Sclerotium rolfsii* are able to hydrolyze xylan, galactoglucomannan, or mannan (91, 108–110). *P. chrysosporium* EG28 has activity toward xylan, mannan, and CMC (91), and EG of *Aspergillus aculeatus* does not hydrolyze cellulose and releases only xyloglucan oligosaccharides from plant cell walls (111). Basidiomycete BGLs from both GH1 and GH3 have been characterized (112, 113). Both basidiomycete and aspergillus BGLs show wide substrate specificity, and they are able to hydrolyze glucose, mannose, xylose, or galactose units from the corresponding oligosaccharides (19, 88).

CDHs are widely present in both basidiomycetes and ascomycetes. In contrast to the other plant cell wall polysaccharide-degrading enzymes, CDHs have been more commonly studied in basidiomycetes than in ascomycetes (114), probably because this enzyme was first found in the white rot fungus *P. chrysosporium* (115). So far, CDHs from 12 different white rot species, the brown rot fungus *C. puteana*, the coprophilic fungus *C. cinerea*, and the plant pathogen *S. rolfsii* have been characterized (Table 8). The average molecular mass of basidiomycete CDHs is 96 kDa (Table 8). The CDHs show acidic isoelectric points (from 3.0 to 6.4) and pH optima (pH 3.5 to 5). The optimum temperature for CDH-catalyzed reactions varies from 50°C to 75°C (Table 8).

The substrate array of the characterized white rot fungal CDHs is variable. *P. chrysosporium* CDH is able to oxidize cellobiose and higher cellodextrins, lactose, mannobiose, and galactosylmannose (29). *C. subvermispora* and *Trametes hirsuta* CDHs are also able to oxidize maltose (116, 117), while CDH of *Irpex lacteus* oxidizes only cellobiose or higher cellodextrins efficiently (118). In addition, the CDHs of *Trametes pubescens* and *Trametes villosa* can oxidize xylobiose (119). The characterized basidiomycete CDHs have pH and temperature optima of 3.5 to 5.5 and 50°C to 75°C, respectively (Table 8). The only characterized brown rot fungal CDH is from *C. puteana*. It oxidizes both cellobiose and cellooligosaccharides but not glucose, which supports the typical catalytic properties of CDH (120, 121).

Basidiomycete and ascomycete CDHs are classified into two subgroups according to their primary amino acid sequences (122). Class I includes basidiomycete CDHs, which are shorter polypeptides than the more complex class II ascomycete CDHs, which have a C-terminal cellulose binding module. In addition, the linker regions in basidiomycete CDHs are more conserved than those in ascomycete CDHs (30). To our knowledge, CDHs from *Aspergillus* species have not been characterized at the protein level to date. The ascomycete CDHs isolated from *N. crassa* have a broader substrate spectrum and less glucose discrimination than basidiomycete CDHs (30). While basidiomycete CDHs catalyze the reactions at acidic pH, ascomycete CDHs are active at neutral or alkaline pH (41). Whether the differences in the biochemical characteristics of CDHs between basidiomycetes and ascomycetes are also valid for *Aspergillus* species remains to be clarified.

Biochemical studies of basidiomycete LPMOs are at the early stage, and most analyses have been conducted only at the gene level (Tables 4 and 8). In fact, enzymes from the white rot fungi *P. chrysosporium* and *H. irregulare* are the only isolated or characterized basidiomycete LPMOs. The structure of *P. chrysosporium* LPMO (GH61D) (PDB accession number 4B5Q) (123) together with five structures of ascomycete LPMOs, i.e., *H. jecorina* (Cel61B) (PDB accession number 2VTC), *Thielavia terrestris* (GH61E) (PDB accession numbers 3EII and 3EJA), *Thermoascus aurantiacus* (GH61A) (PDB accession number 2YET), and *N. crassa* (PMO-2 and PMO-3) (PDB accession numbers 4EIR and 4EIS) LPMOs (27, 28, 33, 124), have opened the path to describing the biochemical properties of various putative LPMOs harbored in fungal genomes.

Currently, cellulose-cleaving activities of LPMOs have been biochemically confirmed only for GH61D of the white rot fungus *P. chrysosporium* (*Pc*GH61D) (125); the above-mentioned ascomycete LPMOs from *H. jecorina*, *T. terrestris*, *T. aurantiacus*, and *N. crassa*; and GH61A and GH61B of the ascomycete fungus *P. anserina* (27, 28, 31, 32, 126, 127). *Pc*GH61D is not active on soluble cellooligosaccharides (125), but it is able to oxidize phosphoric acid-swollen cellulose in the presence of ascorbic acid and to release lactone, which is spontaneously converted to aldonic acid (125). The copper-bound active site that is common to LPMOs is present in *Pc*GH61D (123). Nevertheless, it has significant differences in the loop structures near the binding face compared to the other characterized LPMO structures, which illustrates the diversity of the LPMOs.

Hemicellulose-Degrading Enzymes

Xylan degradation. Xylanases break down the most common hemicellulose found in high quantities in hardwoods and cereals. Of the isolated and characterized basidiomycete xylan-degrading enzymes, 75% are from white rot fungi (Table 9). Moreover, basidiomycetes produce several xylanase isoenzymes, which is also reflected in the high copy number of the corresponding genes present in their genomes (Table 4). The average molecular mass of basidiomycete endoxylanases is 45 kDa (Fig. 3A and Table 9). Their isoelectric points vary from 2.8 to 8.0, and the pH optimum is between 3.0 and 8.0 (Fig. 3B and C and Table 9). Temperature optima for endoxylanase reactions range from 50°C to 80°C (Fig. 3D and Table 9).

GH10 and -11 endoxylanases from some white rot species, the litter-decomposing fungus *A. bisporus*, and the brown rot fungus *G. trabeum* have been characterized (Table 9). Optimum pH values of white rot fungal endoxylanases are most often between 4.0 and 6.0, but an alkaline optimum pH of 8.0 has been reported for *C. subvermispora* endoxylanase (128). *G. trabeum* endoxylanase (*Gt*Xyn10A) also exhibits activity for xyloglucan (129). β-Xylosidases have been isolated from only a few white rot fungal species, including *C. subvermispora*, *G. lucidum*, *P. chrysosporium*, and *Phlebia radiata* (Table 9). The GH43 β-xylosidase of *P. chrysosporium* has a molecular mass of 83 kDa (130), whereas the molecular mass of *P. radiata* β-xylosidase is only 27 kDa (131).

The isoelectric points of xylanases, endoxylanases, and β-xylosidases from aspergilli vary substantially (19). Variation in pI values is also seen in basidiomycetous xylanases, even though the number of characterized enzymes is lower than for ascomycetes (Table 5) (19). Ascomycete xylanases have different specificities toward the xylan polymer, some being strongly dependent on the

TABLE 8 Characterized basidiomycete cellobiose dehydrogenases and lytic polysaccharide monooxygenases, their biochemical properties, and their corresponding genes

Life-style	Species	CAZyme family(ies)	Gene	Enzyme[a]	NCBI protein database accession no.[b]	Molecular mass (kDa)	pI	pH_{opt}[c]	T_{opt}[c] (°C)	Reference(s)
Cellobiose dehydrogenase										
White rot	*Ceriporiopsis subvermispora*	AA3_1, AA8	*cdh*		ACF60617	87–98	3.0	4.5	60	116
	Irpex lacteus			CDHII		97		4.0[d]	50[d]	118
	Phanerochaete chrysosporium		*cdh*		AAC49277	89	4.2	5.0		272, 273
	P. chrysosporium		*cdh*	CDH*	CAA61359	90	4.2	3.5–4[d]		274–276
	Pycnoporus cinnabarinus		*cdh*		AAC32197	92	3.8	4.5	75	277, 278
	P. cinnabarinus			CDHI		81	5.9	5.5		279
	P. cinnabarinus			CDHII		101	3.8	4.5		279
	P. cinnabarinus			CDH*	ADX41688	110		4.5	70	280
	Trametes hirsuta					92	4.2	5.0[e]	60–70	117
	Trametes pubescens			*Tp*CDH		90	4.2	4.5–5.0[e]		119
	Trametes versicolor	AA3_1, AA8	*cdh*	CDH 4.2*	AAC50004	97	4.2	4.5	55	281–283
	T. versicolor	AA3_1		CDH 6.4			6.4		55	281
	Trametes villosa			*Tv*CDH		89	4.4	4.5–5.0[e]		119
	Grifola frondosa		*cdh*	*Gfr*CDH	BAC20641					284
	Phlebia lindtneri		*cdh*		AGE45679	104	4.0	5.0[e]	60[e]	285
	Pycnoporus sanguineus	AA3_1, AA8				113	4.2	4.5	70	286
White rot-like	*Schizophyllum commune*					102				287
Brown rot	*Coniophora puteana*					111	3.9			120, 121
Coprophilic	*Coprinopsis cinerea*	AA3_1, AA8		CDHcc*		~80		5.0	60	114
Plant pathogen	*Sclerotium rolfsii*	AA3_1, AA8				101	4.2–5.0	3.2–4.8	55	288, 289
Lytic polysaccharide monooxygenases										
White rot	*Heterobasidion irregulare*	AA9	*HiGH61A*	GH61A	AFO72232					290
	H. irregulare	AA9	*HiGH61B*	GH61B	AFO72233					290
	H. irregulare	AA9	*HiGH61C*							290
	H. irregulare	AA9	*HiGH61D*	GH61D	AFO72234					290
	H. irregulare	AA9	*HiGH61E*							290
	H. irregulare	AA9	*HiGH61F*		AFO72235					290
	H. irregulare	AA9	*HiGH61G*		AFO72236					290
	H. irregulare	AA9	*HiGH61H*		AFO72237					290
	H. irregulare	AA9	*HiGH61I*		AFO72238					290
	H. irregulare	AA9	*HiGH61J*		AFO72239					290
	Phanerochaete chrysosporium	AA9		*Pc*GH61D*		25	4.8			125

[a] Asterisks indicate a heterologously produced enzyme.
[b] See http://www.ncbi.nlm.nih.gov/protein.
[c] Activity measured with 2,6-dichlorophenolindophenol (DCIP) and cellobiose.
[d] Activity measured with cytochrome *c*.
[e] Activity measured with DCIP and lactose.

substituents of the xylose residues neighboring the attacked residue and others cutting randomly between the unsubstituted xylose residues (19).

Mannan degradation. Only a few basidiomycete mannanases have been characterized compared to cellulases and xylanases (Table 10). However, basidiomycetes provide an avenue for the isolation of unique mannan-degrading enzymes according to their genomes (Table 4). β-Endomannanases have been isolated only from the white rot fungi *P. chrysosporium*, *T. versicolor*, and *C. subvermispora*; the litter-decomposing fungus *A. bisporus*; and the plant pathogen *Sclerotium rolfsii* (128, 132–138). However, mannanase activities have also been measured in other white rot fungi,

TABLE 9 Characterized basidiomycete β-1,4-endoxylanases and β-xylosidases and their biochemical properties

Life-style	Species	CAZyme family	Gene	Enzyme[a]	NCBI protein database accession no.[b]	Molecular mass (kDa)	pI	pH_{opt}	T_{opt} (°C)	Reference
Endoxylanase										
White rot	*Ceriporiopsis* (*Gelatoporia*) *subvermispora*			Xylanase I		79		8.0	50	128
	C. subvermispora					29		5.0	60	291
	Cerrena unicolor					44		4.0		212
	Ganoderma lucidum			Xylanase B		31	5.4			16
	Irpex lacteus					38	7.6–8.0	4.6–5.2	60	292
	I. lacteus			Xylanase I		38		6.0	60	293
	I. lacteus			Xylanase III		62		6.0	70	293
	Lentinula edodes					41	3.6	4.5–5.0	60	294
	L. edodes	GH11	*xyn11A*	XYN11A*	AAL04152			4.5	50	295
	L. edodes	GH10				35		4.0	50	296
	Phanerochaete chrysosporium	GH10	*xynA*	XynA*	ABZ88797	52		4.5	70	297
	P. chrysosporium	GH11	*xynB*	XynB*	ABZ88798	30		4.5	60	297
	P. chrysosporium	GH10	*xynC*	XynC*	ABZ88799	50		4.5	70	297
	P. chrysosporium	GH10	*XynA*	XynA*	AEK97220	50		5.0	70	298
	P. chrysosporium	GH10	*XynC*	XynC*	AEK97221	55		5.0	70	299
	P. chrysosporium	GH10	*XynA*	XYNA*	AAG44992	48				300
	P. chrysosporium	GH11	*XynB*	XYNB*	AAG44995	37				300
	Phlebia radiata			XA-1		19	6.7			131
	P. radiata			XA-2		16	4.1			131
	Pycnoporus cinnabarinus					50	4.0	5.0	60	277
White rot-like	*Schizophyllum commune*	GH11		Xylanase A		33		5.0	55	301
	S. commune	GH10		XynB		31	2.8	5.5	50	302
	S. commune			XynC		30	3.6	5.5	50	302
Brown rot	*Gloeophyllum trabeum*					39–42	5.0	4.0	80	303
	G. trabeum	GH10		Xyn10A		39	4.8			103
	G. trabeum	GH10		Xyn10A*	AFR33046			3.4	50	129
	G. trabeum	GH10		Xyn10B*	AFR33047			4.5	70	129
	G. trabeum	GH10	*Xyl10g*		AEJ35165					—[c]
	Laetiporus sulfureus					69		3.0	80	304
	Postia placenta					43	3.8			305
Litter decomposing	*Agaricus bisporus*	GH10	*xynA*	XLNA*	CAB05665	34				190
Coprophilic	*Coprinopsis cinerea*	GH11		Xyn11C*	AFR33049			6.5	50–60	129
Insect symbiont	*Termitomyces clypeatus*					90		5.5	55	306
	Termitomyces sp.					87		5.6	65–70	307
β-Xylosidase										
White rot	*Phanerochaete chrysosporium*	GH43	*PcXyl*	r*Pc*Xyl*	AFW16059	83		5.0	45	130
	Phlebia radiata			XD-1		27	5.9			131
Plant pathogen	*Sclerotium rolfsii*					170		4.5	50	308

[a] Asterisks indicate a heterologously produced enzyme.
[b] See http://www.ncbi.nlm.nih.gov/protein.
[c] Available in the GenBank database (http://www.ncbi.nlm.nih.gov/GenBank/).

such as *P. ostreatus* (endomannanase [139]) and *P. radiata* (140). The molecular mass of β-endomannanases (42 to 65 kDa) is lower than that of β-mannosidases (49 to 105 kDa), with the exception of the *C. subvermispora* β-endomannanase, with an atypically high molecular mass (150 kDa) (128) (Fig. 3A and Table 10). The isoelectric points have been determined only for the β-endomannanases from *S. rolfsii*, and their pI values are very acidic, from 2.8 to 3.5 (135, 136, 138). Similarly, the pH optima of *S. rolfsii* β-endomannanases are also acidic (pH 2.9 to 3.5), while the optimum pH range for *P. chrysosporium* β-endomannanase is 4.0 to 6.0 (Table 10). β-Mannosidases from the white rot species *G. lucidum* and *P. radiata*, the brown rot fungus *Laetiporus* (*Polypo-*

TABLE 10 Characterized basidiomycete β-1,4-endomannanases and mannosidases and their biochemical properties

Life-style	Species	CAZyme family	Gene	Enzyme[a]	NCBI protein database accession no.[b]	Molecular mass (kDa)	pI	pH_{opt}	T_{opt} (°C)	Reference(s)
β-Endomannanase										
White rot	*Ceriporiopsis* (*Gelatoporia*) *subvermispora*			Mannanase I		150		4.5	60	128
	Heterobasidion irregulare (*Fomes annosus*)						3.9–4.2			309
	Phanerochaete chrysosporium	GH5	*man5D*	Man5D*	ABG79370	65		4.0–6.0	60	132
	P. chrysosporium	GH5	*man5C*		ABG79371					—[c]
	P. chrysosporium (*Chrysosporium lignorum*)						4.11			309
Litter decomposing	*Agaricus bisporus*	GH5	*Cel4b*							133, 134
Plant pathogen	*Sclerotium rolfsii*					61	3.5	2.9	74	135, 136, 310, 311
	S. rolfsii					42	3.2	3.3	72	135, 310
	S. rolfsii					47	2.8	3.0–3.5	75	138
	Stereum sanguinolentum						3.58			309
β-Mannosidase										
White rot	*Ganoderma lucidum*					49	4.2			16
	G. lucidum					49	4.8			16
	Phlebia radiata			GM-1		105	4.8	5.5	50	141
	P. radiata			GM-2		90	3.8	5.5	50	141
	P. radiata			OT-1		100	4.7	5.5	50	141
Brown rot	*Laetiporus* (*Polyporus*) *sulfureus*					64		2.4–3.4		142
Plant pathogen	*Sclerotium rolfsii*					58	4.5	2.5	55	135

[a] Asterisks indicate a heterologously produced enzyme.
[b] See (http://www.ncbi.nlm.nih.gov/protein).
[c] Available in the GenBank database (http://www.ncbi.nlm.nih.gov/GenBank/).

rus) *sulfureus*, and the plant pathogen *S. rolfsii* have been characterized (16, 135, 141, 142); their pI values are close to 4.5, and the optimum pH varies from 2.4 to 5.5 (Fig. 3B and C and Table 10). The average temperature optimum for the β-endomannanases (70°C) is higher than that for β-mannosidases (53°C) (Fig. 3D and Table 10).

Brown rot fungi are specialized in degrading conifers (143), which contain a higher percentage of mannan than hardwoods (20). The genomes of basidiomycetes possess several copies of genes encoding mannan-degrading enzymes assigned to GH2, -5, and -26 (Table 4). Correspondingly, the brown rot fungus *Piptoporus betulinus* has been observed to produce β-mannanase and β-mannosidase activities (109, 144). However, no mannanolytic enzymes from the brown rot basidiomycetes have been isolated or characterized (Table 5). Nevertheless, cellulolytic enzymes of brown rot fungi have been shown to hydrolyze substrates other than cellulose. *Gloeophyllum sepiarium* and *G. trabeum* produce β-1,4-endoglucanases that cleave galactoglucomannan and xylan, respectively (108, 145). *F. palustris* possesses a GH3 β-glucosidase that is active against *p*-nitrophenylxyloside, *p*-nitrophenylgalactoside, *p*-nitrophenylcellobioside, and *p*-nitrophenylmannoside (146). Similarly, *P. betulinus* β-glucosidase is able to release galactose, mannose, and xylose from xylan and galactomannan (109).

Aspergillus species produce both β-endomannanases and β-mannosidases, and characterized enzymes have been classified into GH5 and -2 (19). Altogether, at the level of characterized enzymes, both β-mannanases and β-mannosidases of basidiomycetes and aspergilli have gained less attention than several other CAZymes (Table 10).

Pectin-Degrading Enzymes

Basidiomycete genomes show a high level of variation with respect to pectin degradation (Table 4), but only a few pectinolytic enzymes from basidiomycetes have been characterized (Table 11). Instead, the main focus of studies of pectinases has been on *A. niger* and other *Aspergillus* species. Aspergilli produce variable hydrolases (endo- and exopolygalacturonases, endorhamnogalacturonan hydrolases, rhamnogalacturonan rhamnohydrolase, α-rhamnosidase, and rhamnogalacturonan galacturonohydrolases) and lyases (pectin, pectate, and rhamnogalacturonan lyases), with several isoenzymes that differ in their specific activity (19).

The pectinolytic enzymes of basidiomycetes isolated or characterized so far are endo/exorhamno- or polygalacturonases from the white rot fungus *P. chrysosporium* (147), the plant-pathogenic species *Chondrostereum purpureum* (148–150) and *S. rolfsii* (151, 152), and the basidiomycete yeast *Cystofilobasidium capitatum* (153, 154) as well as a rhamnogalacturonan lyase from the white rot fungus *I. lacteus* (155, 156) (Table 11). However, there is a great

TABLE 11 Characterized basidiomycete pectin-degrading enzymes and their biochemical properties

Life-style	Species	CAZyme family	Gene	Enzyme[a]	NCBI protein database accession no.[b]	Molecular mass (kDa)	pI(s)	pH_{opt}	T_{opt} (°C)	Reference(s)
Endo/exopolygalacturonases and rhamnogalacturonases										
White rot	*Phanerochaete chrysosporium*					42	4.3, 4.6, 4.7	4.7	66	147
Plant pathogen	*Chondrostereum purpureum*	GH28	*epgA*		AAF68401					150
	C. purpureum	GH28	*epgB1*		AAF68402					150
	C. purpureum	GH28	*epgB2*		AAK29433					150
	C. purpureum	GH28	*epgC*		AAF68403					150
	C. purpureum	GH28	*epgD*		AAF68404					150
	C. purpureum	GH28	*cppg1*	PGA	BAA96351					149
	C. purpureum	GH28	*Pg1*	PGA	BAA08102	39	8.8			148
	Sclerotium (*Corticium*) *rolfsii*			PGA				2.5		151
	S. rolfsii					46–48	5.2	4.0		152
	S. rolfsii					28–31	5.2	4.0		152
Yeast	*Cystofilobasidium capitatum*			PGA		44			45	153, 154
Rhamnogalacturonan hydrolase										
White rot	*Irpex lacteus*			RGH*	ACI26689	55	7.2	4.5–5.0	40–50	155, 156

[a] The asterisk indicates a heterologously produced enzyme.
[b] See http://www.ncbi.nlm.nih.gov/protein.

potential to find novel pectinases from basidiomycetes with unique properties because of the diverse ecological niches that basidiomycetes inhabit and the variety of putative pectinase-encoding genes in their genomes (Table 4). For example, several basidiomycetes, including the white rot fungi *Lentinus* sp., *P. chrysosporium*, *Pycnoporus sanguineus*, and *S. commune*, have been shown to produce higher polygalacturonase activities than *A. niger* on solid wheat bran cultures in a screening study of 75 basidiomycetes (63).

The plant pathogens *S. rolfsii* and *C. purpureum* produce an array of GH28 pectinolytic enzymes, which suggests that pectin degradation is important to their pathogenicity (148–150, 157, 158). *C. purpureum*, which causes a silver leaf disease in apple trees, produces five GH28 PGA isoenzymes corresponding to the five cloned PGA-encoding genes (150). A phylogenetic analysis has shown that the PGA-encoding genes of *C. purpureum* have undergone duplication after the divergence of ascomycetes and basidiomycetes, suggesting an adaptation to a pectin-rich environment (150). The pectinases of *S. rolfsii* act under extreme conditions. Pectin methyl esterase (CE8) of *S. rolfsii* has a very acidic pH optimum (pH 2.5) and also retains most of its activity at pH 1.1 and at 10°C (159). In addition, β-galactosidase of *S. rolfsii* tolerates acidic conditions, and its optimum pH is between 2 and 2.5 (151).

Very few pectin- and other plant cell wall polysaccharide-degrading enzymes have been isolated from basidiomycetous yeasts (Tables 5, 7, and 11). This corresponds to the limited number of CAZyme-encoding gene models found in the genome of *R. glutinis* (Table 4). However, the enzymes of basidiomycete yeasts may have interesting biochemical properties. For example, *C. capitatum* uses pectin as a sole carbon source and produces polygalacturonase (GH28), which is active even at 0°C and therefore has potential to be used in food processing applications (153, 154).

Hemicellulose- and Pectin-Debranching Enzymes

Debranching enzymes that cleave the side chains of hemicelluloses and pectin work synergistically with the enzymes that cleave the backbone and main branches of plant polysaccharides (19). Various debranching enzymes from ascomycetes have also been isolated from basidiomycetes, including α- and β-galactosidases, α-arabinofuranosidases, α-glucuronidases, acetyl xylan esterases, a pectin methyl esterase, and feruloyl esterases (Table 12). Despite the putative gene models present in basidiomycete genomes (Table 4), many debranching enzymes from basidiomycetes still remain uncharacterized, such as α-fucosidase, *p*-coumaroyl esterase, arabinoxylan arabinofuranohydrolase, endoarabinase, exoarabinase, and endogalactanase. Due to their importance for the complete degradation of plant biomass, future efforts should be directed at isolating debranching enzymes from basidiomycetes.

Only a few white rot fungal debranching enzymes that catalyze the cleavage of the smaller side branches of hemicellulose and pectin main chains have been characterized (Table 12). *P. chrysosporium* produced α-glucuronidase at high activity levels in a screening study of xylan-degrading fungi, where several ascomycetes, such as *Aspergillus awamori* and *A. niger* strains, and basidiomycetes, such as *P. chrysosporium* and *S. commune*, were included (160). The molecular mass of *P. chrysosporium* α-glucuronidase is 112 kDa, and its isoelectric point is 4.6. It has an acidic pH optimum

TABLE 12 Characterized basidiomycete-debranching enzymes and their biochemical properties

Life-style	Species	CAZyme family	Gene	Enzyme[a]	NCBI protein database accession no.[b]	Molecular mass (kDa)	pI	pH_{opt}	T_{opt} (°C)	Reference(s)
α-Arabinofuranosidase										
White rot	*Dichomitus squalens*					60	5.1	3.5	60	312
Coprophilic	*Coprinopsis cinerea*	GH62	*CcAbf62A*	*Cc*Abf62A*	BAK14423	48		7.0	45	313
α-Galactosidase										
White rot	*Ganoderma lucidum*					49	4.6			16
	G. lucidum					249[c]		6.0	70	166
	Lenzites elegans	GH36				158[d]	4.0–4.2	4.5	60–80	167
	Phanerochaete chrysosporium	GH27			AAG24510, AAG24511	250[c]		3.75		165, 314
	Phlebia radiata			AgaS-b1		60	7.2	5.0	60	169
	P. radiata			AgaS-b2		59	5.7	5.0	60	169
	P. radiata			AgaS-b3		60	3.5	5.0	60	169
	P. radiata			AgaS-m1		55	6.7	5.0	60	169
	P. radiata			AgaS-m2		58	5.7	5.0	60	169
	P. radiata			AgaS-m3		64	5.0	5.0	60	169
	Pleurotus florida					99		4.6–5.0	55	168
Saprobic	*Calvatia cyathiformis*							3.0–5.0	50	315
β-Galactosidase										
Plant pathogen	*Sclerotium* (*Corticium*) *rolfsii*							2.0–2.5		316
Yeast	*Sporobolomyces* (*Bullera*) *singularis*					53		5.0	50	317
β-1,3-Endo/exogalactanase										
White rot	*Flammulina velutipes*	GH16	*FvEn3GAL*	*Fv*En3GAL*	BAK48741	30		5.5	50	318
	Irpex lacteus	GH43	*Il1,3Gal*	r*Il*1,3Gal*	BAH29957	45		4.5	40	319
Galactan β-1,3-galactosidase										
White rot	*Phanerochaete chrysosporium*	GH43	*1,3Gal43A*	1,3Gal43A*	BAD98241	55				320
α-Glucuronidase										
White rot	*Phanerochaete chrysosporium*					112	4.6	3.5		160
	Phlebia radiata					110	4.4	3.8	60	161
White rot-like	*Schizophyllum commune*	GH115	*Agu1*	Agu1*	ADV52250					163
	S. commune					125	3.6	4.5–5.5		162
Litter decomposing	*Agaricus bisporus*							3.3	52	321
Acetyl xylan esterase										
White rot	*Phanerochaete chrysosporium*	CE1	*axe1*							58
	P. chrysosporium	CE1	*PcAxe2*	*Pc*Axe2*	AEX99751	63		7.0	30–35	170
White rot-like	*Schizophyllum commune*					31		7.7	30–45	322
Straw decomposing	*Volvariella volvacea*		*Vvaxe1*	*Vv*AXE1*	ABI63599	45		8.0	60	323
Coprophilic	*Coprinopsis cinerea*[e]		*CcEst1*	*Cc*Est1*	BAJ10857	45				324
Feruloyl esterase										
White rot	*Auricularia auricula-judae*			EstBC		36	3.2	6.5	61–66	175
	Pleurotus eryngii			FaeA		67	5.2	5.0	50	173
	Pleurotus sapidus			Est1		55		6.0	50	174
Pectin methyl esterase										
Plant pathogen	*Sclerotium* (*Corticium*) *rolfsii*					37		2.5–4.5	45	159

[a] Asterisks indicate a heterologously produced enzyme.
[b] See http://www.ncbi.nlm.nih.gov/protein.
[c] Tetramer.
[d] Dimer.
[e] Acetic acid- and ferulic acid-releasing activities.

and hydrolyzes short-chain xylooligosaccharides but shows low activity toward glucuronoxylan polysaccharides and xylans of birch, oat spelt, and wheat straw (160). α-Glucuronidase of the white rot fungus *P. radiata* has been shown to act together with an endoxylanase in the degradation of oat xylan (161). *A. niger* and *A. tubingensis* α-glucuronidases are also active mainly on small xylooligomers, and therefore, they are expected to be dependent on the action of endoxylanases (19). Interestingly, *S. commune* produced an α-glucuronidase that is active against polymeric glucuronoxylan (162) and for which the gene was recently cloned and demonstrated to be a member of GH115 (163). In contrast to this enzyme, a GH115 α-glucuronidase from the ascomycete *Pichia stipitis* was active only on oligomeric substrates (164).

α-Galactosidases have been isolated from some white rot species and have diverse properties. Both *P. chrysosporium* and *G. lucidum* glucomannan-debranching α-galactosidases are produced as tetramers, while the molecular masses of the monomers are 50 and 56 kDa, respectively (165, 166). *P. chrysosporium* α-galactosidase has an acidic pH optimum of 3.75, and the enzyme is stable from 0 to 80°C (165). The pH optimum of *G. lucidum* α-galactosidase is 6.0, and its optimum temperature is 70°C (165, 166) The white rot fungus *Lenzites elegans* secretes a homodimeric α-galactosidase with a molecular mass of 158 kDa (61 kDa for one subunit) (167). α-Galactosidase of *L. elegans* has an acidic pI value ranging from 4.0 to 4.2 and a pH optimum of 4.5. This enzyme shows activity against several α-galactosidases and is very thermostable, with an optimal temperature from 60°C to 80°C (167).

In contrast, α-galactosidase from the white rot fungus *Pleurotus florida* is a monomeric protein with a molecular mass of 99 kDa, and its temperature optimum is 55°C (168). The white rot fungus *P. radiata* produces several isoforms of α-galactosidase when grown in wheat bran- and locus bean gum-containing liquid media (169). Molecular masses of the α-galactosidase isoforms of *P. radiata* are between 55 and 64 kDa, and their isoelectric points vary from 3.5 to 7.15. *P. radiata* α-galactosidase isoforms have an optimum pH of 5.0 and show the highest activity at 60°C (169). Several different α-galactosidases have been purified from aspergilli. In addition, a few endo- and exogalactanases from aspergilli have been characterized (19), but these enzymes have not yet been characterized for basidiomycetes.

Acetyl xylan esterases (AXEs), which cleave ester linkages between acetic acid and xylan or mannan, and feruloyl esterases (FAEs), which cleave ester linkages between phenolic acid and the arabinose or galactose side chain of xylan or pectin, have been characterized for the white rot fungi *P. chrysosporium*, *Pleurotus eryngii*, *Pleurotus sapidus*, and *S. commune*; the jelly fungus *Auricularia auricula-judae*; and the coprophilic species *C. cinerea* (Table 12). The genome of *P. chrysosporium* harbors three AXEs, one of which, *Pc*Axe2, has been biochemically characterized (170). *Pc*Axe2 and AXEs from *Aspergillus ficcum*, *A. awamori*, and *A. niger* show a similar pH optimum (7.0). AXEs of *A. ficcum*, *A. oryzae*, and *A. niger* have slightly higher temperature optima (35°C to 50°C) than that of *Pc*Axe2 (30°C to 35°C) (170–172). *Pc*Axe2 displays low specific activity against birchwood xylan. However, synergistic action between *Pc*Axe2 and the *P. chrysosporium* endoxylanase *Pc*XynC in xylan degradation has been reported (170).

Only three basidomycete FAEs have been biochemically characterized (173–175). The molecular masses of FAEs of the white rot fungi *P. eryngii* and *P. sapidus* are 67 kDa and 55 kDa, respectively, which are higher than those of the FAEs of *A. awamori* (35 kDa) (176) and *A. niger* FaeA (36 kDa) (177, 178) but lower than that of *A. niger* FaeB (74 kDa) (178). *P. eryngii* FaeA (*Pe*FaeA) and *P. sapidus* Est1 are 93% similar at the amino acid sequence level (173). However, they do not show significant homology to *A. niger* FaeA or FaeB, which is also reflected in their biochemical differences. *P. sapidus* Est1 hydrolyzes arabinosyl esters of ferulic acid more efficiently than methyl ferulate, which is the commonly used substrate for feruloyl esterases (174). *Pe*FaeA had higher activity toward natural substrates, such as feruloylated mono-, di-, and trisaccharides (F-A, F-AX, and F-AXG, respectively), than toward the typical synthetic feruloyl ester substrates methyl ferulate, methyl coumarate, and methyl sinapate (173). In addition, it is not able to hydrolyze methyl caffeate (173). Both *Pe*FaeA and *P. sapidus* Est1 prefer F-AX over F-A and F-AXG of the natural substrates, whereas *A. niger* FaeA prefers F-A over F-AX (173, 179). Recently, a novel type of FAE (EstBC), which hydrolyzes both benzoates and cinnamates, has been described for the jelly fungus *A. auricula-judae* (175).

Only two α-xylosidases from *Aspergillus* species (19) and, so far, none from basidiomycetes have been characterized. The α-xylosidases from aspergilli are specific for α-linked xylose residues but show differences in the type of glycosides that they are able to hydrolyze (19, 180, 181).

Several cellulases, xylanases, mannanases, and pectinases have been isolated from phytopathogenic basidiomycetes (Table 5). Most of the characterized enzymes are from *S. rolfsii*, which has a dual life-style as a soil saprotroph and a necrotrophic crop pathogen with a wide host range including >500 plant species (157, 182). *S. rolfsii* causes large economic losses by infecting several crop and ornamental plants, especially in tropical and subtropical regions. During infection, *S. rolfsii* produces oxalic acid as well as cellulolytic and pectinolytic enzymes (157, 182). Although the genome of another necrotrophic basidiomycete, the white rot fungus *H. irregulare*, is already available, the genome of *S. rolfsii* or a related facultative pathogenic basidiomycete has yet to be sequenced to reveal the full genetic potential of phytopathogens for carbohydrate degradation.

REGULATION OF PLANT POLYSACCHARIDE DEGRADATION IN BASIDIOMYCETES AND *ASPERGILLUS*

Considering the highly varied composition of plant biomass, efficient degradation of these components by fungi depends on the production of the right combination of enzymes. Therefore, most genes encoding plant-biomass-degrading enzymes are under the control of transcriptional regulators. In aspergilli, several transcriptional regulators (all of the Zn2Cys6 type) that activate the expression of genes involved in plant biomass degradation have been identified, such as XlnR, AraR, GalR, GalX, and RhaR (183). None of these regulators have orthologs in basidiomycetes, but several are found across the phylum Ascomycota (184). This suggests that regulation of plant biomass degradation has developed after ascomycetes and basidiomycetes diverged during fungal evolution. No specific regulators involved in plant biomass degradation in basidiomycetes have been described, but indications for such systems can be derived from transcriptome studies with basidiomycetes, although these indications were not explicitly stated in those reports (17, 18, 70).

Repression of Gene Expression in Basidiomycetes

CreA-mediated repression is induced by monomeric products such as glucose, fructose, and xylose in ascomycetes (19), but the mechanism has not been studied for basidiomycetes. However, CreA homologs have been detected in all basidiomycete genomes sequenced so far (184). In line with the ascomycetes, various basidiomycetes, such as the white rot fungus *Trametes* (*Coriolus*) *versicolor*, the litter decomposers *A. bisporus* and *V. volvacea*, the phytopathogen *S. rolfsii*, and the basidiomycete yeast *Rhodotorula minuta*, have CAZyme-encoding genes that are repressed by glucose and other monosaccharides (89, 185–188). Some CAZyme-encoding genes are also repressed by monosaccharides that seem unrelated to the enzymes that these genes encode. For example, certain cellulolytic genes are inhibited by lactose, xylose, mannose, and fructose (89, 186, 189). Like ascomycetes, the *xynA* endoxylanase gene of *A. bisporus* is repressed by glucose (190).

Copies of a CreA-related binding site, SYGGRT (191), have been detected in the genomes of basidiomycetes. In the white rot fungus *I. lacteus*, a CreA binding site upstream of the *cel2* gene (GH7 and CBHI) has been found between two CAAT boxes, similarly to what was observed for the *cbhI* gene of *A. aculeatus* (189). CreA binding elements were also identified in the glycosyl hydrolase promoters of the white rot fungi *C. subvermispora* and *S. commune* (12, 163) and the brown rot fungus *P. placenta* (18, 70). However, these elements were not present upstream of the *bglA* gene encoding the β-galactosidase of the basidiomycete yeast *Sporobolomyces singularis* (112). Information from the genomes of basidiomycetes and studies on their genes encoding CAZymes suggests that CreA homologs mediate the repression of some CAZyme-related genes, while other genes are possibly repressed by other mechanisms or constitutively expressed, such as the *cbh1-1* and *cbh1-2* genes from *P. chrysosporium* (192).

To relieve glucose repression at low sugar levels, the Snf1 protein kinase, found in *Saccharomyces cerevisiae* and other ascomycetes (193), targets Mig1, which is a functional homolog of CreA (194). An *snf1* gene has also been identified in the phytopathogen *U. maydis* and was shown to mediate gene expression of at least one EG and one PGA (193). In mutants that did not have *snf1*, EG- and PGA-encoding genes were expressed at lower levels in high concentrations of glucose. However, xylanase gene expression levels were higher in mutants lacking *snf1*. This suggests that Snf1 negatively regulates xylanase expression and is required for the induction of EG- and PGA-encoding genes (193). An ortholog of Snf1, SnfA, has been identified in the brown rot fungus *P. placenta* (18), and it may also exist in other basidiomycetes. However, a direct interaction between Snf1 and CreA has yet to be studied in basidiomycetes.

All these data suggest that CreA homologs in basidiomycetes likely affect the expression of a range of CAZymes and respond to the presence of a variety of monosaccharides, similar to what has been described for *Aspergillus* species (19). The presence of CreA homologs across the fungal kingdom supports a central role for this regulator in fungal physiology in natural habitats (184).

Induction of Gene Expression in Basidiomycetes

CAZyme-encoding genes of basidiomycetes, from the brown rot fungi *F. palustris* and *G. trabeum* to the litter decomposer *A. bisporus*, are induced when exposed to long polymers of cellulose and hemicellulose (105, 186, 195). The CCAAT binding complex, which enhances the expression of genes located downstream of it, is found in the promoter regions of the genes involved in cellulose and hemicellulose degradation in many *Aspergillus* species (19). The white rot fungus *I. lacteus* possesses a CCAAT motif in the promoter region of *cel2* (GH7 and CBHI) (189), which suggests that at least some basidiomycete CAZyme-encoding genes may be upregulated by mechanisms analogous to that of ascomycetes. In the plant pathogen *C. purpureum*, a CCAAT motif was found before the start codon in all five PGA-encoding genes (150). However, not all basidiomycetous CAZyme-encoding genes have a CCAAT binding complex. For example, β-galactosidase of the basidiomycete yeast *S. singularis* does not possess a CCAAT sequence (112).

The expression of multiple genes encoding plant-polysaccharide-degrading enzymes during growth on plant biomass, as evidenced for several basidiomycete species (9, 12, 17, 70, 196), indicates a regulatory system similar to that described for ascomycetes. The absence of homologs of the ascomycete regulators suggests that this may be due to parallel evolution, during which both fungal phyla developed different regulators that perform the same function. This poses an intriguing question regarding how the expression of plant-biomass-degrading enzymes was organized in the ancestral fungi before the divergence of basidiomycetes and ascomycetes.

CONCLUSIONS AND FUTURE PROSPECTS

The increasing number of genome sequences covering the wide range of diversity of biomass-decomposing fungi has widened our understanding of the enzymatic machinery that they possess for plant cell wall polysaccharide degradation. Since the first whole-genome sequencing of a basidiomycete, *P. chrysosporium*, next-generation sequencing has facilitated a growing number of genomes and transcriptomes of plant cell wall-decomposing basidiomycetes (197). These complementary "omics" studies have accelerated the process of discovering novel enzyme activities involved in plant cell wall decomposition. In line with the aspergilli, genome sequencing of basidiomycetes has revealed an unexpectedly large repertoire of GHs. For example, <20% of the putative GHs of *P. chrysosporium* were characterized before the genome sequence was published (59).

At the same time, the genomes of plant-biomass-degrading basidiomycete fungi have revealed putative novel protein-encoding genes, especially among those without known homology, providing enzymes related to plant polysaccharide degradation for further characterization. For instance, several new families, such as the second family of α-glucuronidases (GH115) (163) and a family of glucuronoyl esterases (CE15) (198, 199), have recently been added to the CAZy database. Furthermore, the novel concept of oxidoreductive polysaccharide degradation will provide challenges, as its significance in both the basidiomycete and ascomycete fungi is yet to be fully clarified. The abundance of the LPMO-encoding genes and the diversity of LPMO sequences and described activities for basidiomycetes and other plant-biomass-degrading microorganisms suggest that LPMO-catalyzed oxidation has a major role in plant cell wall polysaccharide conversion (40). The discovery of LPMO changed the concept of cellulose degradation (200, 201), and a recent study demonstrated the ability of LPMO to cleave not only cellulose but also hemicelluloses (40). In the near future, LPMO-catalyzed depolymerization of other plant cell wall polysaccharides besides cellulose and hemicelluloses will most likely be shown. In addition, a new family of

fungal LPMOs from *A. oryzae* was characterized, expanding the substrate range of fungal LPMOs from plant cell wall polysaccharides to chitin (202).

Although genomic approaches have revealed an abundance of putative plant-polysaccharide-degrading enzymes, the number of biochemically characterized basidiomycete CAZymes is still relatively small compared to the number of *Aspergillus* enzymes. For example, representatives of basidiomycete β-galactosidases and endo- and exoarabinases remain to be studied. Future efforts should be directed toward revealing the catalytic potential of basidiomycete CAZymes in biomass utilization by studying enzymes from diverse species. Several complementary techniques have already been employed in secretome studies of basidiomycetes related to lignocellulose degradation (143). However, the number of basidiomycete secretomes examined is still small, and thus, only preliminary conclusions can be drawn. In the future, improved quality of genome assemblies will improve the detection of secreted proteins, thus also clarifying the overall picture of plant polysaccharide degradation (143). This will result in a better understanding of the relationship between fungi and their biotope and will aid in designing new and improved industrial applications.

Together with genomic comparisons between different species, transcriptome and proteome studies have opened up the way to untangle the complex regulatory mechanisms of basidiomycetes that underlie the plant polysaccharide conversion processes. However, more genome sequences are still needed to reveal the full potential and diversity of basidiomycetes for plant biomass degradation. In addition to functional genomics, metabolomics studies combined with knowledge on the regulation of basidiomycete CAZyme-encoding genes will increase our understanding of the complex processes of plant cell wall polysaccharide degradation. It will also facilitate a shift from a descriptive characterization of individual enzymes in plant biomass decay to detailed insight into complex decomposition mechanisms.

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