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Marine woodborers: A source of Lignocellulolytic enzymes

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Abstract

Lignocellulose, the structural framework of woody plants biomass, is an inexhaustible, renewable, and ubiquitous organic material on earth. It is present in huge amounts as agricultural and forestry residues and wastes generated from different industries including solid municipal wastes. Lignocellulosic biomass is an alternative, economical and eco-friendly source for biofuel production and other bio-based products. It is mainly comprised of cellulose, lignocellulose, and lignin polymers. Each of its structural components is degraded by specific enzymes, such as cellulases, hemicellulases and lignolytic enzymes, and these constituents in turn can be utilized as a sustainable source of energy. Biofuel offers great promise to replace fossil fuels without causing the feud of food-fuel supply as they are derived from non-edible sources such as lignocellulosic biomass. For this reason, lignocellulolytic enzymes are the focus of present decade research. These enzymes are obtained from microorganisms especially bacteria, fungi, and actinomycetes. Marine woodborers digest wood and play a role in carbon cycling by bioconversion in the ocean. The woodborers also harbor microbial groups for production of lignocellulolytic enzymes. Various studies have evaluated the lignocellulose degrading ability of marine woodborers and that of microbial groups from their guts, which have potential in the production of value-added products. This paper is an overview of the diversity of marine woodborers endogenous lignocellulolytic enzymes as well as microbial groups from their guts that are sources of lignocellulolytic enzymes, along with a brief discussion on their hydrolytic enzyme systems involved in bioconversion.

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Introduction

Marine woodborers are three groups of invertebrates that biodegrade wood and play a key role in global carbon cycling by processing plant biomass in the ocean. Two of these are mollusks, the first group referred to as shipworms belonging to Family Teredinidae, class Bivalvia; and the second group referred to as piddocks belongs to Family Pholadidae class Bivalvia (Turner, 1966; Turner, 1971). The third group consists of pill bugs, which are arthropods in the class crustacea, order isopoda and family Sphaeromatidae (Pillai, 1961).

Lignocellulose, the structural framework of woody plants biomass, is an inexhaustible, renewable, and ubiquitous organic material on earth. It is present in huge amount as agricultural and forestry residues and wastes generated from different industries including solid municipal wastes. It is composed of three major components: cellulose, hemicelluloses and lignin. (Saini *et al*., 2015; Sokan-Adeaga *et al*., 2016). Each of its structural components is degraded by specific enzymes, such as cellulases, hemicellulases and lignolytic enzymes.

Marine woodborers thrive on a diet of wood, and digest it under ambient temperatures and pressures (Kern *et al*., 2013). Such animals may provide useful understanding of the mechanisms of lignocellulose digestion and provide a source of lignocellulolytic enzymes. In this review, the diversity and application of endogenous lignocellulolytic enzymes and lignocellulolytic microbial groups from marine woodborers have been discussed along with description of their lignocellulolytic enzyme systems involved in bioconversion.

Lignocellulose

Lignocellulose is a major organic structural component of all plants that is renewable. It consists of three major components: two carbohydrate polymers cellulose and hemicellulose; and lignin. In addition, small amounts of various other materials such as ash, proteins and pectin can be found in lignocellulosic residues depending on the source (Sachez, 2009).

Cellulose, the major constituent of all plant material and the most abundant organic molecule on earth, is a linear biopolymer of anhydroglucopyranose molecules, connected by β-1,4-glycosidic bonds. Adjacent cellulose chains are linked by hydrogen bonds, hydrophobic interactions and Van der Waal's forces leading to a parallel alignment of crystal-line structures known as microfibril (Zhang *et al*., 2006; Parthasarathi *et al*., 2011). Cellulose is regarded as the strongest potential candidate for sustainable fuel production due to its renewability, biocompatibility and biodegradability characteristics (Ahn *et al*., 2012; Isikgor and Becer, 2015). Complete depolymerization of cellulose yields just one product, glucose.

Hemicelluloses, the second most abundant component of lignocellulosic biomass, is a heterogeneous polymer of pentoses, hexoses and sugar acids (Saha, 2000; 2003). These are typically five different sugars; L-arabinose, D-galactose, D-glucose, D-mannose, and D-xylose found in conjunction with other components, such as acetic, glucuronic and ferulic acids (Musatto and Teixeira, 2010). Distribution of different sugars in hemicellulose varies with different wood and cultivation conditions. Generally, in soft wood hemicellulosic part is predominantly composed of mannose, which is replaced by xylose in the hard woods (Sorieul *et al*., 2016). Xylan is the major constituent of hemicellulose found in the cell walls of plants and some green and red algae.

Lignin, the third component of lignocellulosic residues is an aromatic heterogeneous polymer made of *p*-hydroxyphenylpropanoid units connected by C–C and C–O–C links. Biosynthetically, lignin arises from three precursor alcohols: *p*-hydroxycinnamyl (coumaryl) alcohol, which gives rise to *p*-hydroxyphenyl units in the polymer; 4-hydroxy-3-methoxycinnamyl (coniferyl) alcohol, the guaiacyl units; and 3, 5- dimethoxy-4-hydroxycinnamyl (sinapyl) alcohol, the syringyl units. Copolymerization of these alcohols, as well as free radicals, produce the heterogeneous, optically inactive, cross-linked, and highly polydispersed polymer. There are over 10 interphenylpropane linkage types, including four that

predominate (Ball *et al*., 1989; Godden *et al*., 1992; Lee, 1997; Weng *et al*., 2008; Bugg *et al*., 2011).

The carbohydrate polymers are tightly bound to lignin mainly by hydrogen bonds but also by some covalent bonds. This prevents penetration of lignocellulolytic enzymes to the interior lignocellulosic structure, since lignin is the most recalcitrant component of lignocellulosic material to degrade (Himmel *et al*., 2007; Sachez, 2009). The biological process of degrading lignocellulose requires delignification to liberate cellulose and hemicellulose from their complex with lignin and depolymerisation of the carbohydrate polymers to produce free sugars. The removal of lignin and releasing fermentable sugars requires pretreatment of lignin followed by enzymatic or acidic hydrolysis of the carbohydrates. (Tengerdy and Szakacs, 2003).

Lignocellulolytic Enzymes

Lignin has been reported to be degradable by several ligninase fungal enzymes. These are lignin peroxidase (LiP), Mn-dependent peroxidase (MnP), and laccase (Lac) or monophenol oxidase (Vaaje-Kolstad *et al*., 2010; Bugg *et al*., 2011; Majumdar *et al*., 2014; Beeson *et al*., 2015; Pollegioni *et al*., 2015; Saini *et al*., 2015; Sokan-Adeaga *et al*., 2016).

Cellulases and hemicellulases are glycoside hydrolases, which are extremely common enzymes with roles in nature including degradation of biomass such as cellulose and hemicellulose. They also perform other cellular functions such as trimming mannosidases involved in N-linked glycoprotein biosynthesis. In addition, together with glycosyltransferases, they form the major catalytic machinery for the synthesis and breakage of glycosidic bonds (Cantrel *et al*., 2009).

Cellulases and most hemicellulases belong to a large group of enzymes known as glycoside hydrolases (GH). GH are classified into EC 3.2.1 as enzymes catalyzing the hydrolysis of O- or S-glycosides. Glycoside hydrolases can also be classified according to the stereochemical outcome of the hydrolysis reaction, whereby they can be classified as either retaining or inverting enzymes (Sinnott, 1990). GH can also be classified as exo- or endo- acting; dependent on whether they act at the end (usually non-reducing) or in the middle, respectively, of an oligosaccharide or polysaccharide chain. They may also be classified by sequence or structure-based methods (Henrissat *et al*., 1995). These have led to 2500 GH that have been identified and classified into 115 families (Davies and Henrissat, 1995; Bairoch, 1999; Coutinho and Henrissat, 1999; Cantrel *et al*., 2009; Kern *et al*., 2013). They are typically named after the substrate that they act upon; thus, glucosidases catalyze the hydrolysis of glucosides and xylanases catalyze the cleavage of the xylose based homopolymer xylan. Glycoside hydrolase (GH) family 11 consist of xylanases.

These enzyme families are found in essentially all domains of life, but they are mainly produced by members from bacteria, fungi, yeast, Actinomycetes and plants with several different activities and specific substrates. However, fungal cellulases (hydrolysis of β-1,4-glycosidic bonds) have been mostly found within a few GH families including 5, 6, 7, 8, 9, 12, 44, 45, 48, 61 and 74 (Sandgren *et al*., 2005; Cantrel *et al*., 2009; Saini *et al*., 2015).

Complete enzymatic hydrolysis of cellulose requires action of a cellulolytic enzyme complex containing at least three types of glucanase. These are endoglucanase or endo-β-1, 4-D- glucanase (EC 3.2.1.4); exoglucanase or exo-β-1, 4-D-glucanase or exo-β-1, 4-D-cellobiohydrolase (EC 3.2.1.91) and β-D -glucosidase or cellobiase (β-D-glucoside glucanohydrolase) (EC 3.2.1.21) (de Vries and Visser, 2001; de Vries, 2003; Watanabe and Tokuda, 2010; van den Brink and de Vries, 2011; Payne *et al*., 2015; Kuhad *et al*., 2011).

Complete degradation of hemicellulose heteropolymer requires endoxylanase (EC 3.2.1.8), β-xylosidase (EC 3.2.1.37), acetylxylan esterase (EC 3.1.1.72), L-arabinose releasing enzymes such as α-L-arabinofuranosidase (EC 3.2.1.55) and arabinoxylan arabinofuranohydrolase, α-glucuronidase (EC 3.2.1.139), feruloyl esterase, and *p*-coumaroyl esterase (Sunna and Antranikian, 1997; Gregory *et al*., 1998; Biswas, 2014; Sajith *et al*., 2016).

The major constituents in lignocellulose enzyme hydrolysates are glucose and xylose released from cellulose and hemicellulose, respectively (Himmel, 2007; Hahn-Hagerdal *et al*., 2007; Galazka *et al*., 2010, and de Souza, 2013).

Potential Application of Lignocellulolytic enzymes

Lignocellulose can be used to produce chemicals such as biofuels. It is a cheap energy source for fermentation, improved animal feed (reduce the fibre content to improve feed utilization) and human nutrients (Howard *et al*., 2003; Gravatis, 2004; Madson and Tereck, 2004). The enzymatic hydrolysis of lignocellulose, hemicellulose and cellulose results in production of hexose and pentose sugars as well as various lignin monomers. Glucose is a common substrate used in the fermentation processes for industrial products such as organic acids, amino acids, vitamins and several bacterial and fungal polysaccharides. Xylose, produced from saccharification of hemicellulose, is used in the production of xylitol and furfural.

The fermentation of the sugars from cellulose and hemicellulose degradation generates products such as ethanol, acetone, butanol, glycerol, acetic acid, citric acid and fumaric acid. These chemicals, along with aromatic compounds produced from the hydrolysis of lignin, can be used to make other organic chemicals, which in turn can be used to produce various chemical products including polymers and resins (Howard *et al*., 2003). Ethanol and butanol produced from degraded and fermented lignocellulose can be used as biofuels.

Bioethanol converted from edible sources such as corns and sugarcane is classified as first-generation bio-ethanol (FGB), whereas that produced from non-food sources is classified as second-generation bio-ethanol (SGB). SGB offers great promise to replace fossil fuels without causing a food-fuel supply feud since they are derived from non-edible sources such as lignocellulose biomass (Chun *et al*., 2010).

Cellulases and hemicellulases and ligninases make up a large portion of the world‘s industrial enzymes due to their wide range of uses in various industries. Industrial uses include chemicals, fuel, food, brewing and wine, animal feed, textile and laundry, pulp and paper, and agriculture. Xylanases are used in the baking industry to improve the texture, volume and shelf life of bread and for wheat separation. Xylitol is used as an artificial sweetener in food, in teeth hardening, and as an anti-microbial agent in toothpaste and chewing gum. Furfural is used in manufacturing furfural-phenol plastics, varnishes and pesticides (Howard *et al*., 2003; Gravatis, 2004).

Sources of Lignocellulolytic enzymes

Lignocellulolytic enzymes are produced by a number of microbes, including fungi, bacteria and actinomycetes (Dashtban *et al*., 2009; Bandounas *et al*., 2011; Saini *et al*., 2015).

Lignocellulolytic Bacteria

A variety of bacteria biodegrade lignocellulose (Bandounas *et al*., 2011). Members of the genus Bacillus have been reported to have either ligninolytic or cellulolytic activities or both. These include *B. pumilus*, *B. brevis*, *B. alcalophilus*, *B. subtilis*, *B. cereus*, *B. licheniformis*, *B. circulans*, *B. atrophaeus*, *B. halodurans*, *B. tequilensis* and *B. polymyxa* (Anand *et al*., 2009; Bandounas *et al*., 2011; Ahmad *et al*., 2013; Huang *et al*., 2013; Dubey *et al*., 2014; Prasad *et al*., 2014; Woo *et al*., 2014; Behera *et al*., 2014). *Klebsiella variicola* has lignocellulolytic activities and can utilize diverse types of carbohydrates (Jiménez *et al*., 2014; Dantur *et al*., 2015; Islam *et al*., 2017). *Acinetobacter calcoaceticus* and other Acinetobacter members utilize lignin as carbon sources (Ghodake *et al*., 2009; Ponnambalam *et al*., 2011; Ho *et al*., 2017). *Stenotrophomonas sp.* and *Proteus vulgaris* are cellulolytic (Anand *et al*., 2009; Dubey *et al*., 2014). *A. calcoaceticus* (*A. pittii*), *A. baumannii*, *K. variicola*, *Chryseobacterium gleum*, *Bacillus spp*., and *Stenotrophomonas maltophilia* have been found to have the ability to degrade both lignin and cellulose (Ahmed *et al*., 2018).

Bacterial laccases have been reported in a few *Bacillus species* (*B. tequilensis*, *B. atrophaeus* and *B. pumilus*) (Bandounas *et al*., 2011; Huang *et al*., 2013; de Gonzalo *et al*., 2016). These have been shown to

have both intracellular and extracellular laccase activities (Huang *et al*., 2013; de Gonzalo *et al*., 2016).

Lignocellulolytic enzyme-producing Fungi

Lignocellulolytic enzymes-producing fungi are numerous and widespread. They include species from the Ascomycetes (e.g. *Trichoderma reesei*), basidiomycetes including white-rot fungi (e.g. *Phanerochaetes chrysosporium),* brown-rot fungi (e.g. *Fomitopsis palustris*) and a few anaerobic species (e.g. *Orpinomyces sp.*), which degrade cellulose in gastrointestinal tracts of ruminant animals (Ozkose *et al*., 2001).

Dashtban *et al*. (2009) categorizes different fungi producing lignocellulolytic enzymes into two groups; aerobic fungi (Ascomycetes and Basidiomycete), which produce extracellular lignocellulolytic enzymes and anaerobic fungi, which are cell-wall associated lignocellulolytic enzymes (cellulosomes).

Ascomycetes which have been reported to produce mainly cellulases and hemicellulases, include *T. reesei* (Chahal, 1985, Kurzatkowski *et al*., 1996), *T. harzianum* (Sivan *et al*., 1984, Khan *et al*., 2007), *Aspergillus niger* (Park *et al*., 2002) and *Pestalotiopsis sp.,* which produces laccase in addition to cellulases (Hao *et al*., 2006; Hao *et al*., 2007).

Basidiomycetes, which have been reported to produce cellulases, hemicellulases as well as lignolytic enzymes, include *P. chrysosporium* (Baldrian and Valaskova, 2008; Abbas, 2008; Sanchez, 2009) and *Fomitopsis palustris* (Yoon *et al*., 2007; Song *et al*., 2008).

The anaerobic fungi, which have been reported to produce majorly cellulases and hemicellulase, include *Anaeromyces* (Lee *et al*., 2001; Doi, 2008), *Caecomyces* (Roger *et al*., 1992, Gerbi *et al*., 1996, Doi, 2008), *Cyllamyces* (Ozkose *et al*., 2001; Doi, 2008), *Neocallimastix* (Li and Calza, 1991; Doi, 2008; Griffith *et al*., 2009), *Orpinomyces* (Chen *et al*., 1998; Ljungdahl, 2008, Doi, 2008, Griffith *et al*., 2009) and *Piromyces* (Roger *et al*., 1992; Ali *et al*., 1995; Ljungdahl, 2008; Doi, 2008).

Biomass degradation by these fungi is performed by complex mixtures of cellulases (Bayer *et al*., 1998), hemicellulases (Sachez, 2009) and ligninases (Weng *et al*., 2008; Sachez, 2009) due to the complexity of the materials. Genes involved in lignocellulose degradation during composting of agricultural wastes have been identified in Streptomyces to be a two-domain laccase-like multicopper oxidase genes (Lu *et al*., 2014).

Lignocellulolytic Actinomycetes

Actinomycetes belong to order Actinomycetales, a separate taxonomic group within domain bacteria (Chaudhary *et al*., 2013). They are Gram positive bacteria, mainly aerobic and spore forming (Jeffrey, 2008). They exhibit filamentous growth and produce aerial or substrate mycelium, features they share with fungi (Das *et al*., 2012). Being both mesophilic and thermophilic groups (Wilson, 1992), they have a wide range of habitats and thus are ubiquitous in nature, occurring in both aquatic habitats such as mangroves and sea sediments as well as terrestrial environments (Veiga *et al*., 1983; Chaudhary *et al*., 2013; Das, *et al*., 2014).

Actinomycetes have been reported to produce cellulases, hemicellulases and lignolytic enzymes. High cellulase activity has been reported by a number of studies (Kluepfel *et al*., 1986; Saini *et al*., 2015). Hemicellulase activity, mainly xylanase in actinomycetes has been the most extensively studied in the last four decades, especially in streptomyces (Kusakabie *et al*.,1977; McCarthy *et al* ., 1985; Kluepfel *et al*., 1986; Morosoli *et al*., 1986; Ball and McCarthy, 1988; Roberts *et al*., 1990; Fernández *et al*., 1995; Hernández-Coronado *et al*., 1997; López-Fernández *et al*., 1998; Beg *et al*., 2000; Sharma and Bajaj, 2005; Rifaat *et al*., 2005; Maryandani, 2007; Khurana *et al*., 2007; Ninawe *et al*., 2008; Shin *et al*., 2009; Bajaj and Sing, 2010; Jeffrey *et al*., 2011; Bhosale *et al*., 2011; Padmavathi *et al*., 2011; Abdel-Aziz, 2011; Boroujeni *et al*., 2012; Priya *et al*., 2012; Thomas *et al*., 2013a; Thomas *et al*., 2013b).

Other hemicellulolytic Actinomycetes reports include *Microbispora siemensis* (Boondaeng *et al*., 2011), *Microtetraspora flexuosa* (Berens *et al*., 1996),

Thermoactinomyces thalophilus subgroup C (Kohli *et al*., 2001) and *Thermomonospora sp* (Ristroph and Humphrey, 1985).

Specific hemicellulolytic activity in Actinomycetes have been reported by a number of studies. These are endoxylanase (Grabski and Jeffries, 1993; Grabski *et al*., 1993), β-xylosidase (van Zyl,1985; Ball and McCarthy, 1988), acetyl xylan esterases and α-L-arabinofuranosidases enzymes (Tsujibo *et al*., 2004), acetylesterases and arabinofuranosidases (Ball and McCarthy, 1988) and hemicellulolytic mannanase enzyme (Jeffrey and Azrizal, 2007).

Lignolytic activity by a diverse range of Actinomycetes has also been reported in several studies. Laccase (Gunne and Urlacher, 2012; Fernandes *et al*., 2014a, 2014b) from superfamilies I and K; and laccase, manganese peroxidase, and lignin peroxidase (Ramachandra *et al*., 1988; Iqbal *et al*., 1994; Niladevi and Prema, 2005; Roes-Hill, 2011; Jing and Wang, 2012) lignin modifying enzymes (Sutherland *et al*., 1979; Pometto and Crawford, 1986; Rüttimann *et al*., 1987; Ball *et al*., 1989; Pasti *et al*., 1990; Godden *et al*., 1992; Mason *et al*., 2001; Strachan *et al*., 2012; Escudero *et al*., 2012). Among the lignolytic enzymes, laccase is the most extensively studied and purified for various applications (Arias *et al*., 2003; Niladevi *et al*., 2008; Mahmoud *et al*., 2013; Chen *et al*., 2013; Santo *et al*., 2013; Fernandes *et al*., 2014a, 2014b; Aoyama *et al*., 2014).

Marine Woodborers' Endogenous Lignocellulolytic enzymes

Bosire *et al*. (2013a) investigated lignocellulolytic activities of the gut extracts of the marine woodboring organisms Dicyathifer mannii. The ligninolytic activities investigated were lignin peroxidase (LiP), manganese-dependent peroxidase (MnP) and laccase (Lac) or monophenol oxidase. Cellulolytic enzymes investigated were glucanases endoglucanase (endo-1-4-β-D-glucanase), exoglucanase (1,4-β-D-glucan-cellobiohydrolase), and β-D-glucosidase or cellobiase (β-D-glucoside glucanohydrolase). Endo-1-4-β-xylanase (hemicellulolytic enzyme) was also investigated in the hydrolysis of xylan, the chief type of hemicellulose. *D. mannii* crude extracts showed an appreciable Lip activity of up to 34.65±0.116U/L and endoglucanase (CMCase) activity of up to 50.7U/ml.

The woodboring Crustacean *Sphaeroma terebrans* gut contents have been reported to exhibit cellulolytic enzyme activity. This has been attributed to their hepato-pancreatic secretions which include cellulase. The marine woodborers are thought to be attracted to the fungi in the wood (Geyer and Becker, 1980). The fungi add nitrogen to their largely cellulose diet. Complete cellulose digestion is thought to be accomplished by symbiotic bacteria, the hindgut playing a major role in the digestive process (Hassall and Jennings, 1975).

Limnoriid wood borers have been claimed to have no microbes in the digestive tract, suggesting that they produce endogenous enzymes necessary for lignocellulose digestion (Kern *et al*., 2013). *Limnoria quadripunctata*, a wood borer, which is unusual in having a digestive tract free of microbial life, has a gut with an inert chitinous lining in which free radical chemistry is deployed as a pretreatment for enzymatic hydrolysis. Enzymes are produced in a separate organ and transposed to the gut, which functions as an enzyme reactor (King *et al*., 2010; Kern *et al*., 2013; Besser *et al*., 2018).

L. quadripunctata has revealed a transcriptome dominated by glycosyl hydrolase genes encoding putative cellulases, including glycosyl hydrolase family 7 (GH7) (LqCel7B) cellobiohydrolases (King *et al*., 2010, Besser *et al*., 2018). This GH7 has been used to reveal the mechanisms of cellulase salt tolerance in the wood borer (Kern *et al*., 2013).

A study by Sabbadin *et al*. (2018) using a combination of transcriptomics, proteomics, and microscopy of the shipworm *Lyrodus pedicellatus* gut contents showed that the digestive proteome of the woodborer is mostly composed of enzymes produced by the animal itself, with a small but significant contribution from symbiotic bacteria. The digestive proteome was found to be dominated by a novel 300kDa multi-domain glycoside hydrolase that functions in the hydrolysis of β-1,4-glucans, the most abundant polymers in wood.

The study on *L. pedicellatus*, as well as previous studies on non-marine wood-feeding invertebrates such as cockroaches, beetles, and termites (Watanabe and Tokuda, 2010; Brune, 2014; Cairo *et al*., 2016), suggest that a combination of endogenous and symbiotic enzymes is optimal for efficient plant cell wall digestion in these organisms. It is interesting to note that the genomes of insects, crustaceans, annelids and molluscs encode numerous enzymes involved in plant cell wall digestion. This implies that some of these genes were present in the last common ancestor of bilaterian animals (Calderón-Cortés *et al*., 2012), before bacterial symbioses developed. This would likely represent an ancestral mechanism for lignocellulose digestion, where they share a complex array of endogenous lignocellulolytic enzymes. For instance, *L. pedicellatus* relies mostly on GH9s, GH45s, and GH1s to breakdown terrestrial woody plants, the same is probably true for most shipworm species, which typically feed on submerged wood (Popper *et al*., 2011).

L. pedicellatus cecum meta-proteome, has led to the discovery that the most abundant enzyme in woodborers' digestive tract is an unusual multi-modular GH1 with sequence similarity to the lactase phlorizin hydrolase (LPH) found in mammals. Unlike the mature peptide in the mammalian LPH, which has two GH1 domains linked by a short peptide and which is mostly active as a β-glucosidase, the *L. pedicellatus* MDGH1 has six domains, and has specificity against β-linked glucosides as well as complex glucans. This suggests the ability to cleave these linkages in cellulose and glucomannans during wood digestion (Sabbadin *et al*., 2018).

Marine Woodborers' Microbial Groups with Lignocellulolytic Activities

Bosire *et al*., (2013b) isolated and characterized closely related members of bacteria of the genus *Lysinibacillus* from three marine woodborers. These were *L. boronitolerans* (from *D. mannii a*nd *S. terebrans*), *L. fusiformis* (from *S. terebrans* and *Cirolana sp.), L. sphaericus* and *L. xylanilyticus* (both from *Cirolana sp.)*. In the same study, *Ascomycetes* fungi were also isolated and characterized from marine woodborers gut. *Aspergillus niger* was isolated from the digestive tracts of *D.mannii* and *S. terebrans*. *Neosartorya fischeri*, *A. fumigatus* and *Penicillium sp.* were isolated from *D. mannii* whereas *Botryotinia fuckeliana* was isolated form *S. terebrans* digestive tract. *A. costaricaensis* and *A. fumigatus* were isolated from *Cirolanna sp.* digestive tract. The bacterial and fungal strains of *Lysinibacilli* and *Aspergilli* were found to have a high potential for β-glucosidase and xylanase activity (Bosire and Laila, 2017).

A large amount of carbohydrate active enzymes (CAZymes) have been shown to be produced by endosymbiotic bacteria housed in specialized cells (bacteriocytes) in the marine woodborer *L. pedicellatus* and *Bankia setacea* (O'Connor *et al*., 2014).

Using Fluorescence In-Situ Hybridization (FISH) and laser scanning confocal microscopy with 16S rRNA directed oligonucleotide probes targeting domains of bacteria, archaea, and other taxonomic groups, the digestive microbiota of 17 specimens from five shipworm species (*B. setacea*, *L. pedicellatus*, *L. massa*, a *Lyrodus sp.* and *Teredo aff. triangularis*) were examined (Betcher *et al*., 2012). These data reveal that the caecum, a large sac-like appendage of the stomach that typically contains large quantities of wood particles, is the primary site of wood digestion. It harbors only very sparse microbial populations, but has a significant number of bacterial cells in fecal pellets within the intestines. This suggests a possible role for intestinal bacteria in the degradation of lignocellulose. In several shipworm species, dense communities of intracellular bacterial endosymbionts have been observed within specialized cells (bacteriocytes) of the gills (ctenidia). These bacteria are proposed to contribute to digestion of wood by the host.

In a study on community-based lignocellulose degradation of wheat straw in liquid cultures using a metasecretome approach combined with metatranscriptomics analysis, Alessi *et al*. (2018) extracted 1127 proteins. These proteins revealed the presence of numerous carbohydrate-active enzymes from the biomass- bound fractions and from the

culture supernatant of a microbial community**.** These enzymes revealed a wide array of hydrolytic cellulases, hemicellulases and carbohydrate-binding modules involved in lignocellulose degradation. Therefore, microbial communities that efficiently breakdown plant materials in nature are species rich and secrete numerous enzymes that perform "community-level" metabolism of lignocellulose. Single-species approaches are unlikely to capture all aspects of lignocellulose degradation that will be key to optimizing commercial processes (Alessi *et al*., 2018).

The study undertaken by Sabbadin *et al.* (2018) on the digestive system of *L. pedicellatus* has revealed the complex molecular mechanisms of lignocellulose digestion in shipworms. The digestive gland produces a complex enzymatic mixture containing most of the activities required for the digestion of the plant cell wall, including cellulases (endo-β-1,4-glucanases, β-glucosidases) and hemicellulases (β-mannanases (mannosidases), β-xylanases (xylosidases). Although the meta-transcriptome of *L. pedicellatus* lacks endogenous cellobiohydrolases (CBHs), studies on *B. setacea* reveal presence of gill bacteria GH6s (which can act as CBHs) that enable a digestive strategy in wood-feeding molluscs (O'Connor *et al*., 2014).

In addition, expression of bacterial lytic polysaccharide monooxygenases (LPMOs) and bacterial glucanases were also detected, which likely synergize endogenous enzymes. LPMOs have been shown to insert breaks into highly crystalline polysaccharides thereby enhancing the activity of glycoside hydrolases in a large magnitude (Vaaje-Kolstad *et al*., 2010; Quinlan *et al*., 2011; Leggio *et al*., 2015).

Early work by Distel and Roberts (1997) discussed the role of bacterial endosymbionts found in gill tissue in several bivalve families. The bacterial endosymbionts were reported to convert energy sources (sulfides, methane and cellulose) to form readily metabolized products by the hosts. Existence of such symbionts were investigated in two Xylophaga species; *X. atlantica* and *X. washingtona* (Family Pholadidae). Using transmission and electron microscopy, endosymbionts resembling shipworm endosymbionts both in morphology and in their anatomical location within the gills were identified. This suggests that *Xylophaga* has evolved a symbiotic mechanism for wood digestion similar to that seen in shipworms (Distel and Roberts, 1997).

Future Prospects

It's evident from this review that some studies on marine woodborers' endogenous lignocellulolytic enzymes (Geyer and Becker, 1980; King *et al*., 2010; Popper *et al*., 2011; Kern *et al*., 2013; Bosire *et al*., 2013a; Besser *et al*., 2018; Sabbadin *et al*., 2018) as well as microbial groups from their guts that are sources of lignocellulolytic enzymes (Distel and Roberts 1997; Betcher *et al*., 2012; Bosire *et al*., 2013b; O'Connor *et al*., 2014; Bosire and Laila, 2017; Sabbadin *et al*., 2018; Alessi *et al*., 2018) have been undertaken, and their hydrolytic enzyme systems involved in bioconversion have been discussed. These studies are majorly focused on two of the three groups of marine woodborers; the shipworms (Family Teredinidae) and pill bugs (Family Sphaeromatidae). Studies on piddocks (Family Pholadidae) are scanty, limited to lignocellulolytic enzymes in *Xylophaga* (Distel and Roberts, 1997). Therefore, molecular profiling of microbial groups from piddocks' guts as well as endogenous enzymes secreted from digestive glands as potential sources of lignocellulolytic enzymes of importance is imperative.

Lignocellulose represents the most abundant and ubiquitous organic material in nature. The breakdown of this recalcitrant polymer plays a critical role in the global carbon cycle, and is attracting growing interest from a biotechnological perspective. Society needs to moves away from the use of net greenhouse gas-emitting fossil resources, the use of surplus woody biomass to provide fuels, chemicals, and materials. Unravelling the mechanisms entailed in the digestive systems of major wood-digesting animals provides insight into enzymes that could help towards effective and efficient breakdown of lignocellulosic biomass into simple sugars and other building blocks.

There seems to be a lignocellulose degradation mechanism across the tree of life (Popper *et al*., 2011; Calderón-Cortés *et al*., 2012; Cragg *et al*., 2015), where organisms use diverse mechanisms involving multiple complementary enzymes, particularly glycoside hydrolases (GHs) (Sandgren *et al*., 2005; Cantrel *et al*., 2009; King *et al*., 2010; Kern *et al*., 2013; O'Connor *et al*., 2014; Sabbadin *et al*., 2018; Besser *et al*., 2018), to deconstruct lignocellulose. This knowledge is priceless in the future of designing and engineering enzymes to use in lignocellulose degradation.

Lytic polysaccharide monooxygenases (LPMOs) are produced by bacteria, fungi and Actinomycetes to facilitate deconstruction of lignocellulosic biomass (Dashtban *et al*., 2009; Bandounas *et al*., 2011; Saini *et al*., 2015). Lignin depolymerization is achieved by fungi and certain bacteria, using peroxidases and laccases (Arias *et al*., 2003; Sachez, 2009; Huang *et al*., 2013; de Gonzalo *et al*., 2016). Lignocellulose-consuming animals secrete some GHs (O'Connor *et al*., 2014). Protists from termite guts and some oomycetes produce multiple lignocellulolytic enzymes, but also most harbour a diverse enzyme-secreting gut microflora in a mutualism that is particularly complex in termites (Watanabe and Tokuda, 2010; Brune, 2014; Cairo *et al*., 2016). Shipworms house GH-secreting and LPMO-secreting bacteria separate from the site of digestion (Vaaje-Kolstad *et al*., 2010; Quinlan *et al*., 2011; Leggio *et al*., 2015; Sabbadin *et al*., 2018) and the isopod Limnoria relies on endogenous enzymes alone (King *et al*., 2010; Kern *et al*., 2013; Besser *et al*., 2018). The omics (metatranscriptomic, proteomic) revolution is able to identify many novel enzymes and paradigms for biomass deconstruction (Abbas *et al*., 2005; Sabbadin *et al*., 2018; Alessi *et al*., 2018). Meta-omics is now revealing the complexity of prokaryotic degradative activity in lignocellulose-rich environments. This wealth of knowledge is crucial, however, more emphasis on function is required, particularly for enzyme cocktails, in which LPMOs may play an important role (Sørensen *et al*., 2013).

The sustainability of biorefineries relies on the identification of the most effective enzymatic cocktails for bioconversion. This could help engineer an optimal enzymatic cocktail for biomass bioconversion of lignocellulosic waste. In addition, shipworms seem to have overcome the issue of cellobiose accumulation, which is a potent inhibitor of endo-glucanases and cellobiohydrolases. They overcome this by mass production of a unique multi-domain hydrolase with dual activity towards long-chain glucans and cellobiose. This is an elegant evolutionary solution that should be kept in mind, which will help simplify the enzymatic cocktails used in cellulosic biorefineries (Sørensen *et al*., 2013).

Elucidation of marine woodborers digestomics, which define the collective pool of host and symbiont genes that collaborate to achieve a high-efficiency lignocellulose digestion is essential. The high efficiency of marine woodborers gut bioreactors makes them promising models for the industrial conversion of lignocellulose into microbial products, enzymes and enzyme combinations of potential value to bioconversion (Bosire and Abubakar, 2017).

Conclusion

Marine woodborers are an important source of endogenous and microbial lignocellulolytic enzymes. The microbial groups can also be exploited from a variety of other ecological niches where they occur naturally. The genetic and protein studies on their lignocellulolytic enzymes can lead to the elucidation of structural and mechanism details of the enzymes and their relatedness with other known lignocellulolytic enzyme systems. Recent studies have provided crucial information on endogenous marine woodborers lignocellulolytic enzymes as well as lignocellulolytic enzymes produced by microbial groups from marine woodborers guts. Research studies therefore, need to be done in view of utilization of marine woodborers and lignocellulolytic potential of microbial groups from marine woodborers applicable in different industrial and other sectors. Enormous information is available on microorganisms, primarily bacteria, fungi and ascomycetes that produce lignocellulolytic enzymes,

however, marine woodborers lignocellulolytic enzymes have not been studied as extensively.

Despite some progress achieved, more efforts are required to improve catalytic activities and production efficiency of lignocellulolytic enzymes through genetic engineering and molecular modeling that can have significant industrial impact.

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