



Research review paper

# Lignocellulose-degrading enzymes from termites and their symbiotic microbiota

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## ABSTRACT

Lignocellulose—the dry matter of plants, or “plant biomass”—digestion is of increasing interest in organismal metabolism research, specifically the conversion of biomass into biofuels. Termites efficiently decompose lignocelluloses, and studies on lignocellulolytic systems may elucidate mechanisms of efficient lignocellulose degradation in termites as well as offer novel enzyme sources, findings which have significant potential industrial applications. Recent progress in metagenomic and metatranscriptomic research has illuminated the diversity of lignocellulolytic enzymes within the termite gut. Here, we review state-of-the-art research on lignocellulose-degrading systems in termites, specifically cellulases, xylanases, and lignin modification enzymes produced by termites and their symbiotic microbiota. We also discuss recent investigations into heterologous overexpression of lignocellulolytic enzymes from termites and their symbionts.

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## 1. Introduction

Lignocellulose, mainly comprised of cellulose, hemicelluloses, and lignin, is the most abundant biomass on earth and is recognized as a potential sustainable source for biofuels and biomaterial production

(Himmel et al., 2007; Ragauskas et al., 2006). Termites, which are efficient lignocellulose decomposers, thrive on dead plant materials and contribute to carbon mineralization, especially in tropical and subtropical regions (Kudo, 2009; Ohkuma, 2003; Yamada et al., 2005). Studies to elucidate termite lignocellulose-degrading systems should identify many cellulose hydrolysis enzymes and enhance our understanding of mechanisms of lignocellulose degradation in termites (Scharf and Tartar, 2008). Such investigations may also contribute to optimization of plant biomass bioconversion processes. Therefore, termite biomass degradation has received significant interest in the

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last decade. Using “termite” and “enzyme” as key words to search the National Center for Biotechnology Information's database of biomedical literature (PubMed) we found 238 papers: 230 manuscripts dated from 2000 to the present (November 27, 2012) and 38 papers published prior to 2000 (1978–1999). Such findings indicate the increased research emphasis in the biology of termite enzymes for the last 10 years.

Termites (Isoptera or Termitoidea) are well-studied social insects, considered to be an epifamily of the cockroach (Blattaria or Blattodea). The diversity and classification of termites are well documented elsewhere (Eggleton, 2011; Lo and Eggleton, 2011), so we have briefly summarized important facts here. Termite group is comprised of more than 2600 described species, leaving perhaps 500–1000 species currently undescribed (Eggleton, 2011). Termites are generally classified into seven families: Mastotermitidae, Kalotermitidae, Termopsidae, Hodotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae (Lo and Eggleton, 2011). The Mastotermitidae are the most primitive family, containing only one wood-feeding species in Australia. Termites of the Kalotermitidae family consume material from dry wood, and Termopsidae nest in and feed on wet dead logs. Hodotermitidae are grass-harvesters, and Rhinotermitidae consume wood, primarily in temperate zones. Serritermitidae contains few species and only in South America, suggesting that they may be better classified within the Rhinotermitidae family (Eggleton, 2011). Termitidae is the largest family, consisting of approximately 2000 species and accounting for almost 75% of all known termites. Termitidae consists of at least seven sub-families, namely Macrotermitinae, Sphaerotermitinae, Foraminitermitinae, Apicotermitinae, Termitinae, Syntermitinae, and Nasutitermitinae (Eggleton, 2011; Lo and Eggleton, 2011). Termitidae have diverse feeding preferences, the majority feeding on soil. A few subfamilies such as Termitinae, Nasutitermitinae, and Syntermitinae contain wood- or litter-feeding termites. Termites of the sub-family Macrotermitinae cultivate basidiomycete fungi (*Termitomyces* sp.) in their nests, and are thus commonly known as fungus-growing termites.

Based on the presence or absence of flagellated protistan symbionts in the hindgut of termites, they are conventionally grouped into lower and higher termites. The first six families, all of which harbor protistan symbionts in the hindgut, are referred to as “lower termites”. The remaining family, Termitidae, which lack protistan symbionts in the hindgut, are traditionally referred to as “higher termites” (Lo and Eggleton, 2011).

Studies of cellulose digestion in termites and related insects and the historical importance of these findings have been well-documented elsewhere (Hongoh, 2011; Lo et al., 2011; Matsui et al., 2009; Watanabe and Tokuda, 2001, 2010). In this review, we have focused on the lignocellulolytic system in termites, with special reference to lignocellulose-degrading enzymes such as cellulases, xylanases, and laccases produced by termites and their symbiotic microbiota. We also describe enzyme gene resources, heterologous overexpression systems, and relevant enzyme properties that hold promise for industrial applications.

## 2. The termite intestinal tract

The intestinal tracts of termites are axially structured microenvironments with differences in metabolic activities and microbial community structures (Köhler et al., 2012). The termite gut generally consists of the foregut, midgut, and hindgut. The foregut is an esophageal tract of ectodermal origin with an enlarged anterior segment (“the crop”) and a posterior segment (“the gizzard”) that plays a role in mechanical grinding of ingested wood fragments. The midgut, which in insects is chiefly a secretion site for digestive enzymes and nutrient absorption, is columnar and uniform with an endodermal origin. The midgut is located posterior to the foregut. The Malpighian tubules are usually attached to the end of the midgut to excrete nitrogen wastes to the gut lumen. The hindgut,

of ectodermal origin, is the largest organ. The hindgut can be further subdivided into P1, P2, P3, P4, and P5 segments (Watanabe and Tokuda, 2010). Among these segments, P3 is typically enlarged to harbor numerous microorganisms. The gut microbial community contains all three domains of organisms: Archaea, Bacteria, and Eukaryotes (protists). Relatively little microbiota is found in the foregut and midgut, whereas abundant microbiota is found in the hindgut (Hongoh, 2011; Köhler et al., 2012). The hindgut compartments of higher termites are more developed and complex than those of lower termites. Except for Macrotermitinae, Sphaerotermitinae, and Foraminitermitinae, higher termites have developed a “mixed segment” (half of the gut wall consists of midgut tissue; the remaining is hindgut tissue) between the midgut and the hindgut, but the precise function of the mixed segment has not been elucidated. In addition to the intestinal tract, the salivary glands also significantly contribute to the digestive physiology of termites. Detailed descriptions of termite gut structures are documented elsewhere (see Bignell, 1994, 2011; Lo and Eggleton, 2011 and references therein).

## 3. Cellulose and cellulase

Lignocellulose consists of cellulose (20–50%), hemicellulose (15–35%), and lignin (18–35%). Cellulose, a linear polysaccharide consisting of  $\beta$ -1,4-linked D-glucopyranosyl units, is the major component of plant material (20–40%) and the most abundant biomass on earth (Tomme et al., 1995). Cellulases, found in the gut of lower and higher termites, are produced by organisms that catalyze the cellulolysis (or hydrolysis) of cellulose, and three classes have been identified in cellulolysis. Endo- $\beta$ -1,4-glucanases (EC 3.2.1.4) hydrolyze cellulose chains in a non-processive (random) manner, whereas exoglucanases such as cellodextrinases (EC 3.2.1.74) or cellobiohydrolases (EC 3.2.1.91) depolymerize cellulose chains from their reducing or non-reducing ends in a processive or ordered manner.  $\beta$ -Glucosidases (EC 3.2.1.21) cleave cello-oligosaccharides (especially cellobiose) to liberate glucose.

### 3.1. Cellulolytic systems in lower termites

Distribution patterns of cellulolytic enzymes in the gut of termites have been studied extensively, but relevant studies on soil-feeding termites are limited. The distribution patterns and expression of cellulolytic enzymes in the termite gut varied by termite caste and developmental stages (Fujita et al., 2008; Shimada and Maekawa, 2010). Thus, this review focuses on mature worker-caste termites that feed on lignocellulosic materials and have significant digestive roles among the castes. Generally, lower termites possess strong hydrolytic activity (45–85% of total gut activity) against carboxymethyl-cellulose (CMC) (representing endo- $\beta$ -1,4-glucanase [EG] activity) in the salivary glands (Tokuda et al., 2004), whereas these termites possess stronger cellulolytic activity (40–88%) in the hindgut than in the salivary glands when microcrystalline cellulose is the substrate (primarily representing cellobiohydrolase [CBH] activity) (Tokuda et al., 2005). Regarding  $\beta$ -glucosidase (BG), lower termites have stronger enzymatic activities both in the salivary glands and the hindgut than higher termites (Slaytor, 2000; Tokuda et al., 2002). The relevant genes encoding these enzymes have been identified (Lo et al., 2011; Watanabe and Tokuda, 2010). Based on peptide sequence similarities, glycoside hydrolases are classified into more than 100 families (see <http://www.cazy.org>). Members of the same family frequently have different substrate specificities but share structural similarities that, in turn, reflect their evolutionary origins (Henrissat and Bairoch, 1993). According to this classification, all endogenous EGs are affiliated with the glycoside hydrolase family (GHF) 9 (Leonardo et al., 2011; Tartar et al., 2009; Watanabe and Tokuda, 2010; Zhang et al., 2012b), while all endogenous BGs belong to GHF1, except for one putative endogenous GHF3 BG which has been identified from the salivary gland EST library of *Hodotermopsis sjostedti* (Termopsidae)

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