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INSECT DIGESTIVE GLYCOSIDASES: STRATEGIES OF PURIFICATION, BIOCHEMICAL PROPERTIES AND POTENTIAL APPLICATIONS, A REVIEW

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A B S T R A C T

Insects are animal of extraordinary ecological and economic importance. In these ones, digestive glycosidases are to play a key physiological role in maintenance, survival and reproduction. Moreover, these enzymes were extensively investigated in terms of purification, biochemical and molecular characterization and potential application as tools in glycobiology. This review focuses on amylolytic, cellulolytic and xylanolytic enzymes in insects in order to provide some data on purification strategies, biochemical and molecular properties and potential applications. These digestive glycosidases from insects are generally α-amylase and α-glucosidase, endoglucanase and β-glucosidase, xylanase and β-xylosidase for amylolytic, cellulolytic and xylanolytic enzymes, respectively. Their purifications are done using ammonium sulphate precipitation followed by chromatographic steps as gel filtration, ion-exchange and hydrophobic interaction. Their biochemical characterization indicated generally optimum pH and temperature values between 3.5 and 10.0 and 30 and 60°C, respectively. Molecular characterization in terms of molecular weight estimation indicated that these enzymes are generally medium in size with molecular weights of less than 200 kDa. Regarding their applications, some of these enzymes could be useful for saccharification of glucose polymers in order to produce syrup of oligosaccharides mixture, when others could be the valuable tools for the synthesis of oligosaccharides and neoglycoconjugates by transglycosylation reactions and also in biotechnological application and biofuel production. But also, in particular, α-amylases are used as a target for the control of pest insects.

Keywords: Insect, digestive glycosidases, α-amylase, α-glucosidase, endoglucanase, β-glucosidase, endoxylanase, β-xylosidase, purification, characterization, application.

INTRODUCTION

Insects represent the dominant group in the world fauna and in ecological and economic points of view, these invertebrates are important. They are a class of invertebrates within the phylum Antropoda with a remarkable dietary diversity (Ruppert *et al*., 2004). Some are plant feeders named herbivores and xylophages feeding on leaves, roots, stems, grains and the carnivores or entomophagous individuals that are those insects feeding on other insects. Digestive enzymes are well documented to play a key role in maintenance, survival and reproduction in insects (Oyebanji *et al*., 2014). These digestive enzymes show similarities both in structure and function to those found in vertebrates (Penzlin, 1999). They constitute hydrolases which cut nutrient molecules at a specific site by inserting a water molecule. In insects, the nature of the digestive enzymes secreted is associated with the nature of the meal that they can assimilate (Hubert *et al*., 1999; Agusti and Cohen, 2000; Zeng and Cohen, 2000a; Torres and Boyd, 2009, Tierno de Figueroa *et al*., 2011). Particularly for herbivorous insects, these are glycosidases mostly secreted in the midgut and salivary gland (Agrawal and Bahadur, 1978). These hydrolases ensure the hydrolysis of the carbohydrate macromolecules such as starch, cellulose and hemicelluloses present in plant organs ingested by insects. Several reports indicated rightly that insects that constituting serious pests of stored grains depend to a large extent on the effectiveness of their α-amylases for their survival (Mendiola-Olaya *et al*., 2000; Peligrini *et al*., 2006; Bandani *et al*., 2010). Interestingly,

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the ability of some insects to survive on wood, foliage and detritus has naturally stimulated some investigations to understand how such species can digest cellulose and hemicelllulose as xylan. Among these different investigations, termites have emerged as insects having the best efficient of cellulose (Abo-Khatwa, 1978; Martin and Martin, 1979) and hemicellulose digestion (Krishna, 1969). A large number of studies have been devoted to determining amylolytic, cellulolytic and xylanolytic activities in insects. The digestives α-amylases of insects that constitute serious pests for stored grains or certain plant species were studied in the first time to gain a better understanding of their digestive physiology, which will lead to new strategies of control (Mendiola-Olaya *et al*., 2000; Peligrini *et al*., 2006; Dojnov *et al*., 2008; Ahmadi *et al*., 2012). Then, digestive cellulase and xylanase were analyzed in herbivorous and xylophagous insects such termites in order to have elements that can help to understand the process of cellulose and hemiceluloses digestion in insects. Although insect cellulose digestion has traditionally been hypothesized to occur through enzymes produced by symbiotic gut microbes in insects (Martin, 1983), an evidence has also supported a crucial role for endogenous cellulolytic enzymes in some insects (Nakashima *et al*., 2002; Tokuda *et al*., 2007; Zhou *et al*., 2008; Willis *et al*., 2011, Zhang *et al*. 2011). In addition, various studies have reported endogenous insect cellulases in insect orders Blattaria, Coleoptera, Hymenoptera, Hemiptera, Phthiraptera, and Orthoptera (Watanabe and Tokuda, 2010). To date, insect xylanases are known to be secreted by symbiotic gut microorganisms such as bacteria, fungus, protozoa (Rouland *et al*., 1988; Faulet *et al*., 2006a: Heo *et al*., 2006). The insect glycosidases are currently purified and characterized to find new sources of enzymes with similar properties to microorganism enzymes with various applications (Kouamé *et al*., 2005a; Faulet *et al*., 2006b, Yapi *et al.,* 2009, Kouadio *et al*., 2012). The present review is intended to take stock of amylolytic, cellulolytic and xylanolytic enzymes in insects by indicating their purification strategies, biochemical and molecular properties and potential applications.

PURIFICATION STRATEGIES OF SOME AMYLOLYTIC, CELLULOLYTIC AND XYLANOLYTIC ENZYMES FROM INSECT: In order to determine their biochemical and molecular properties, the insect glycosidases need to be purified. In most cases, purification strategies have involved classical purification methods. These methods involve preparation of the crude extract, selective concentration by precipitation using generally ammonium sulphate or in a few cases the organic solvent such as chilled acetone. The crude enzyme is then subjected to chromatography, usually gel filtration (size exclusion), ion exchange and hydrophobic interaction chromatography. As shown in Table 2, the literature on the purification of insect glycosidases is extremely provided. Methods of the crude extract preparation are numerous. Whilst some reports indicated the preparation of the crude extract from homogenate of the whole digestive tract of insect (Sugimura *et al*., 2003; Kouadio *et al*., 2010) or its various compartments (salivary glands, midgut, foregut or hindgut) (Marana *et al.*, 2000; Zeng and Cohen, 2000; Dojnov *et al*., 2008, Xue *et al*., 2008; Arakawa *et al*., 2009; Zibaee *et al*, 2012), others showed that this preparation was performed from homogenate of the whole bodies of insect (Podoler and applebaum, 1971; Tanimura *et al*., 1979; Mendiola-Olaya *et al*., 2000; Kouamé *et al.,* 2005a, 2005b; Faulet *et al.*, 2006; Wongchawalit *et al*., 2006; Cinco-Moroyoqui *et al*., 2008; Binaté *et al*., 2008; Wisessing *et al.*, 2008; Rehman *et al*., 2009) and isolates from symbiotic microorganisms (Faulet *et al*., 2006a: Heo *et al*., 2006) or simply, by using the digestive fluid (Nagaraju and Abraham, 1995; Yapi *et al*., 2009). The use of these different purification strategies has led to the obtaining of enzymatic preparations with purities confirmed by electrophoresis analysis. In some cases, the reports devoted to purification of insect glycosidases showed the existence of multiple isoforms, mainly regarding α-amylase (Dojnov *et al*., 2008, Cinco-Moroyoqui *et al*., 2008), α-glucosidase (Tanimura *et al.*, 1979) and β-glucosidase (Marana *et al.*, 2000, Kouamé *et al*., 2005b). Regarding the purification fold and recovery yields, the important observation is that these purification parameters vary depending on the purification strategy and the enzyme source.

BIOCHEMICAL PROPERTIES: The biochemical and molecular properties of amylolytic, cellulolytic and xylanolytic enzymes from several insects have been extensively studied and described. Generally, these investigations have focused on the optimum conditions (pH and temperature optima), molecular weight, the effect of some metal ions (inhibitors and activators) and chemical agents as sulphydryl group reagents, chelating agent (EDTA) and others, substrate specificity.

Table 1. Strategies of purification of amylolytic, cellulolytic and xylanolytic enzymes from insects. Abbreviation: NP – Not provided.

Insect species	Activity	Crude extract preparation	Purification strategy	Fold purification/ Yield (%)	Reference
Callosobruchus chinensis (Coleoptera: Chrysomelidae)	α-amylase	Supernatant obtained after homogenization of larvae in 0.02 M sodium acetate buffer, pH5.4, containing 0.05 mM calcium Nitrate; followed by centrifugation at 60,000 g for 20 min.	Cold precipitation and precipitate discarded after centrifugation at 60,000 g for 20 min; co-precipitation as a glycogen-amylase complex at 5 °C, followed by centrifugation at 7,000 g for 10 min, anion-exchange chromatography on ECTEOLA-cellulose column.	NP/NP	Podoler and applebaum (1971)
Drosophila melanogaster (Diptera: Drosophilidae)	α-glucosidase	Homogenization of whole bodies of flies in 0.05 M potassium phosphate buffer, pH 7.3, containing 0.1 M KCl, 0.4 mM DTT, 1 mM EDTA, and 0.5 mM phenylmethylsulfonyl fluoride, then gentle stirring for 3 h , and the supernatant obtained after centrifugation at 22,000 g for 1 h was removed and stored.	75 % $(NH_4)_2SO_4$ precipitation; con A-Sepharose 4B affinity chromatography; For α-glucosidase I and II (adsorbed on con-A sepharose): DEAE-Sepharose CL-6B chromatography; Sephacryl S-200 gel filtration; Preparative polyacrylamide gel electrophoresis. For α-glucosidase III (non- adsorbed on con-A sepharose): DEAE-Sepharose CL-6B chromatography; Sephacryl S-200 gel filtration; rechromatography on DEAE Sepharose CL-6B; Preparative polyacrylamide gel electrophoresis	α-glucosidase I: 600/2.1 α-glucosidase II: 940/5.4 α-glucosidase III: 1200/5.7	Tanimura *et al.* (1979)
Macrotermes mülleri (Isoptera: Termitidae)	Endoglucanase	Whole bodies of termite workers were homogenized with 15 ml 0.9 % NaCl solution and then sonicated. The homogenate was centrifuged at 13,000 g for 15 min. The collected supernatant constituted the crude extract.	Hydroxyapatite adsorption, DEAE Sepharose, Mono Q chromatographies: molecular sieving column Superose 12.2.2.	NP/NP	Rouland *et al.* (1988)
Prostephanus Truncates (Coleoptera: Brostrichidae)	α-amylase	Extract obtained after homogenization of whole larvae in 0.01 M Tris–HCl (pH 7.2) followed by filtration through paper Whatman No. 4.	Q-Sepharose, Econo Pac High Q chromatographies; Preparative electrophoresis; Sephadex G-75 gel filtration.	1209/8.7	Mendiola-Olaya *et al.* (2000)
Spodoptera frugiperda (Lepidoptera:	β-glycosidase	Insect guts were dissected in cold 125 mM NaCl, and the midgut tissue was pulled apart. Midgut	Gel filtration on Superose 12 HR 10/30 column, Ion exchange chromatography on Mono Q HR 5/5 column, Hydrophobic	A1: 71/12 A2: 395/30	Marana *et al.* (2000)

Noctuidae)		tissue, after being rinsed thoroughly with saline, was homogenized in double distilled water, frozen-and-thawed three times and centrifuged at 25,000g for 30 min at 4°C. The supernatant was stored at 220°C until use.	chromatography on Alkyl Superose HR 5/5 column.		
Lygus hesperus and *L. lineolaris* (Hemiptera: Miridae)	α-amylase	Salivary glands complexes of adult insects were dissected and ground in phosphate buffer with a glass homogenizer. The homogenates were centrifuged at 10, 000 rpm for 10 min at 4°C, and supernatants were pooled and stored at 20°C for later purification	Ion-exchange chromatography on Econo-Pac-S column, Isoelectric focusing.	NP/NP	Zeng and Cohen (2000b)
Apis mellifera (Hymenoptera : Apidae)	β-glucosidase	After dissection of insects, honey sacs or ventriculus were mashed with a glass rod in 5 ml of phosphate buffer pH 7.4. Then, the mixture was centrifuged for 30 minutes at 6,000 g and filtered through glass wool This solution constituted the raw extract.	70-90 % $(NH_4)_2SO_4$ precipitation, anion-exchange chromatography on DEAE Sepharose, cation-exchange chromatography on CM Sepharose, High Performance cation-exchange on Mono S, hydroxyapatite chromatography, High Performance Gel Filtration on Superose 12.	38.2/NP	Pontoh and Low, (2002)
Psacothea Hilaris (Coleoptera: Cerambycidae)	Endoglucanase	Whole guts of larvae were homogenized in sodium acetate buffer pH 5.5 using a glass homogenizer, and centrifuged at 10,000 g for 10 min; the supernatant obtained was the crude extract.	Cold-acetone precipitation, elution from gels after native PAGE and SDS/PAGE with activity staining.	NP/NP	Sugimura *et al.* (2003)
Macrotermes subhyalinus (Isoptera: Termitidae)	β-glycosidase	Whole bodies of termite workers were homogenized with 15 ml 0.9 % NaCl solution and then sonicated. The homogenate was centrifuged at 13,000 g for 15 min. The collected supernatant constituted the crude extract.	80 % $(NH_4)_2SO_4$ precipitation; Sephacryl S-100 HR gel filtration, DEAE-sepharose CL-6B, Phenyl-Sepharose CL 6B chromatographies.	β-gly A: 31.43/02.45 β-gly B: 61.00/ 07.97	Kouamé *et al.* (2005b)

Periplaneta Americana (Blattodea: Blattidae)	α-glucosidase	Supernatant obtained after whole bodies grinding followed by centrifugation at 7,000 g for 20 min.	Sephacryl S-100 gel filtration; DEAE sepharose, phenyl-sepharose chromatographies.	79.19/22.73	Kouamé *et al.* (2005a)
Macrotermes subhyalinus (Isoptera: Termitidae)	Endo-xylanase	Supernatant obtained after homogenization and sonication of symbiotic fungi Termitomyces sp in 0.9% NaCl, followed by centrifugation at 15,000 g for 15 min at 4°C.	DEAE-Sepharose CL-6B, CM-Sepharose CL-4B chromatographies; Sephacryl S-200 HR gel filtration; Phenyl Sepharose CL-4B chromatography.	55/2.0	Faulet *et al.* (2006a)
Macrotermes subhyalinus (Isoptera: Termitidae)	Endo-xylanase	Supernatant obtained after disruption and sonication of worker in NaCl 0.9 % , followed by centrifugation at 15,000 g for 15 min at 4 °C.	DEAE-Sepharose CL-6B chromatography, Sephacryl-S 200 HR gel filtration, CM-Sepharose CL-6B, Phenyl-Sepharose CL-4B chromatographies.	114.6/1.0	Faulet *et al.* (2006b)
Apis cerana Japonica (Hymenoptera: Apidae)	α-glucosidase	Whole bodies of honeybees were homogenized in phosphate buffer pH 6.3. After stirring in overnight at 4 °C, the homogenate was centrifuged at 15,500 g for 15 min. Supernatant obtained was the crude extract	100 % $(NH_4)_2SO_4$ precipitation, Salting-out column chromatography; CM-Toyopearl 650M column chromatography; Sephacryl S-100HR gel filtration.	NP/49	Wongchawalit *et al.* (2006)
Morimus Funereus (Coleoptera: Cerambycidae)	α-amylase	Supernatant obtained after dissection and homogenization of midguts, followed by centrifugation at 50,000 g for 10 min.	Two cycles of chromatography on Sephadex G 100; DEAE Sepharose CL-6B chromatography.	112/15.4	Dojnov *et al.* (2008)
Reticulitermes flaviceps (Isoptera: Rhinotermitidae)	β-glucosidase	Salivary glands of termite workers were collected and sonicated, then, the sample was centrifuged at 48,400 g for 10 min and the supernatant was collected and used as crude extract.	High Q anion-exchange chromatography, CM cation-exchange chromatographies; Sephadex G-100 gel filtration.	48.83/8.34	Xue *et al.* (2008)
Rhyzopertha dominica (Coleoptera: Bostrichidae)	α-amylase	Maceration of adults in mortar in 20 mM Tris–HCl, pH 7, containing 20mM NaCl and 10mM $CaCl_2$ followed by homogenate filtration through 0.45 μm nylon filters.	25% $(NH_4)_2SO_4$, then 75% $(NH_4)_2SO_4$, precipitation; Phenyl-sepharose chromatography.	RdA90: 4.5/2.7 RdA79: 53.8/22.1 Rda70: 48.4/21.0	Cinco-Moroyoqui *et al*. (2008)

Macrotermes bellicosus (Isoptera: Termitidae)	β-glucosidase	Whole body of termite workers were homogenized with 15 ml 0.9 % NaCl solution and then sonicated. The homogenate was centrifuged at 13,000 g for 15 min. The collected supernatant constituted the crude extract.	DEAE-Sepharose CL-6B chromatography; 80 % $(NH_4)_2SO_4$ precipitation; Sephacryl S-200 HR gel filtration; Phenyl Sepharose CL-4B chromatography.	Beta-Glc A: 39.43/11.67 Beta-Glc B: 125.46/26.53	Binaté *et al.* (2008)
Callosobruchus maculatus (Coleoptera: Chrysomelidae)	α-amylase	Whole bodies of insect were finely grounded in cold mortar in sodium phosphate buffer pH 7 and centrifuged at 10,000 g for 20 min. The supernatant was used as the crude extract.	β-cyclodextrin sepharose 6B affinity chromatography column.	52/2	Wisessing *et al.* (2008)
Rhynchophorus palmarum (Coleoptera: Curculionidae)	β-glucosidase	Dissection of larvae guts in cold 0.9 % KCl, removal and stirring of digestive content, followed by centrifugation at 6000 x g for 30 min, then stirring of the supernatant with 100 mM acetate buffer pH 5.0 and supernatant obtained after centrifugation at 10,000 x g for 30 min was the crude extract.	DEAE-Sepharose CL-6B chromatography; 80 % $(NH_4)_2SO_4$ precipitation; Sephacryl S-100 HR gel filtration; Phenyl-Sepharose CL-6B chromatography.	36.38/4.47	Yapi *et al.* (2009)
Tribolium Castaneum Coleoptera: Tenebrionidae)	Endoglucanase	Homogenization of whole bodies of insect in phosphate buffer pH 7.0. Homogenate was centrifuged at 10,000 rpm for 15 min and the supernatant constituted the crude extract	Ice-cold acetone precipitation, gel filtration on sephadex G-75 column, ion-exchange chromatography on DEAE-sephadex column	NP/NP	Rehman *et al.* (2009)
Coptotermes formosanus (Isoptera: Rhinotermitidae)	Endoxylanase	Dissection of the salivary glands and the whole gut; the gut was divided into foregut, migut and hingut; salivary glands and each of the gut sections were homogenized in 100 mM sodium acetate buffer pH 5.5 at 4 °C. The samples were then centrifuged at 20,000 g for 15 min at 4 °C. Supernatants diluted with the buffer constituted the crude extracts.	Ion-exchange chromatography on HiLoad 26/10 SP Sepharose High Perfomance Column, then on 5/50 Mono-S Column, Gel filtration on HiLoad 16/60 Superdex 200.	CfXyn1: 204/0.5 CfXyn2: 346/5.0 CfXyn3: 416/3.0	Arakawa *et al.* (2009)

Gryllodes sigillatus (Orthoptera: Gryllidae)	α-amylase	Supernatant obtained after homogenization of digestive tract, followed by centrifugation at 6,000 g, for 20 min at 4 °C	80 % $(NH_4)_2SO_4$ precipitation; Sephacryl S-100 HR, DEAE-sepharose CL-6B, Phenyl-Sepharose 6 Fast-flow chromatographies.	Amy A1: 60.61/ 23.28 Amy A2: 58.55/ 26.00	Kouadio *et al*. (2010)
Andrallus spinidens (Hemiptera: Pentatomidae)	α-amylase	Salivary glands were separated from the insect body, placed in a pre-cooled homogenizer and grounded. Homogenate was centrifuged at 13,000 rpm for 15 min at 4 °C. The supernatant were pooled and stored at -20 °C.	40 and 80 % $(NH_4)_2SO_4$ precipitation; gel filtration on Sepharyl G-100 column; ion-exchange chromatography on DEAE-cellulose.	13.83/14.67	Zibaee *et al.* (2012)

pH optima: Generally, the pH optima of α-amylases prospected in insect vary from 4.0 to 10.0. Number of reports indicated that insect α-amylases are generally more active in neutral to slightly acid pH conditions: Podoler and applebaum (1971) (pH 5.2-5.4); Buonocore *et al*. (1976) (pH 5.8); Baker (1991) (pH 7.0); Cohen and Hendrix (1994) (pH 7.0); Mendiola-Olaya *et al.* (2000) (pH 6.0); Dojnov *et al.* (2008) (pH 5.2); Dué *et al.* (2008) (pH 5.6); Wisessing *et al.* (2008) (pH 5.0-6.0); Mehrabadi and Bandani (2009) (pH 6.5-7.0); Kouadio *et al.* (2010) (pH 6.6 and 7.0); Priya *et al.* (2010) (pH 7.0); Riseh *et al*.(2012) (pH 4.0-5.0); Ahsaei *et al.* (2013) (pH 5.0). However, insect α-amylases, with alkaline pH optima have also been reported: Nagaraju and Abraham, (1995) (pH 9.5); Pytelkova *et al.* (2009) (pH 9.0-10.0); .Asadi *et al.* (2010) (pH 8.0 and 9.0); Bandani *et al.* 2010 (pH 10); Zibaee *et al.* (2012) (pH 9.0); Chitgar *et al.* (2013) (pH 8.0); Darvishzadeh *et al.* (2013) (pH 8.0)].With regard to insect α-glucosidase, Most of the pH optima values were 5.0 (Takewaki *et al*., 1980; Wongchawalit *et al*., 2006; Kouamé *et al*., 2005a; Bandani *et al*., 2010; Sharifi *et al.,* 2011; Riseh *et al.,* 2012; Aghaali *et al*., 2012) or in range from 5.5 to 7.0 [Tanimura *et al*., 1979 (PH 5.5 and 6.5); Fonseca *et al*., 2010 (pH 6.0).

As for the cellulolytic enzymes, a number of reports on endoglucanases have indicated that most of activities occur in neutral and slightly acidic conditions. Thus, insect endoglucanases with pH optima of 4.4 (Rouland *et al*., 1988), 4.5 (Rehman *et al*., 2009), 5.0 (Kim *et al*., 2008; Uddin *et al*., 2012), 5.5 (Sugimura *et al*., 2003; Hirayama *et a*l., 2010), 5.8 (Tokuda et al., 1997), 6.0 (Azuma *et al*., 1984), 6.0 and 7.0 (Sajjadian *et al*., 2012) have been reported. Furthermore, it is worth noting the particular case of endoglucanases from beetle *Mylabris pustulata* which have a very acidic pH optima of 2.0 and neutral pH of 7.0 (Sami *et al*., 2011). However, there are a few insect endoglucanases with alkaline pH optima reported in the literature [Sami and Shakoori, 2008 (pH 7.8); Willis *et al*., 2011 (pH 8.5)]. As regards insect β-glucosidases, they also exhibit pH optima in the range of slightly acidic to neutral like the insect endoglucanases.Thus, β-glucosidases with pH optima values of 4-5.5 (Dehghanikhah *et al*., 2014), 5.0 (Pontoh and Low, 2002; Yapi *et al*., 2009, Uchima et al., 2011; Ahsaei *et al*., 2013; Chitgar *et al*., 2013), 5.2-6.0 (Xue *et al*., 2008), 5.4 (Kouamé *et al*., 2005), 5.6 (Tokuda *et al*., 2002), 5.6-6.2 (Zhang *et al*., 2012), 6.0 (Binaté *et al*., 2008, Uchima *et al*., 2013), 6.2 (Ferreira and Terra, 1983), 6.7, 6.3, and 7.2 (Azevedo *et al*., 2003) have been characterized in various insect species. Endoxylanase and β-xylosidase which constitute the main characterized xylanolytic enzymes among insect, showed in the most cases their maximum activities in pH range from 4.5 to 7.0. Thus, many authors have purified endoxylanases from insect digestive tract or from isolates of symbiotic fungus or bacteria with pH optima values included in this pH range: Matoud and Rouland (1995) (pH 5.0), Roy *et al.* (2003) (pH 7.0), Heo *et al*. (2006) (pH 6.0), Faulet *et al*., (2006a) (pH 5.0-5.6), Faulet *et al*. (2006b) (pH 5.6), Ratnadewi *et al* (2007) (pH 5.0), Blé*i et al*. (2011) (pH 5.0), Anand *et al*. (2010) (pH 7.0), Padilla-Hurtado *et al*. (2012) (pH 5.5), Mattéoti *et al*. (2012) (pH 5.0). In addition, insect endoxylanases with alkaline pH optima (pH 8.0 and 11.0) have been described from microbial DNA isolated from

termites and moths intestinal tract (Brennan *et al*., 2004). For, insect β-xylosidase, it was poorly characterized in terms of pH effect. However, a few β-xylosidases with acidic pH optima have been characterized among termites *Coptotermes formosanus* (pH 5.0) (Azuma *et al*., 1984) and *Reticulitermes santonensis* (pH 6.0) (Mattéotti *et al.*, 2011) or beetle *Holotrichia parallela* (pH 6.0) (Sheng *et al*., 2014).

Temperature optima: Most of characterized α-amylases among insect are mesophilic enzymes which display temperature optima values ranging from 20 to 60 °C: Buonocore *et al*. (1976) (35 °C), Mendiola-Olaya *et al*. (2000) (30 °C), Pelegrini *et al*. (2006) (20-30 °C), Wisessing *et al.* (2008) (50-60 °C), Dojnov *et al*. (2008) (45 °C), Kouadio *et al*. (2010) (55 °C), Priya *et al*. (2010) (40 °C); Omotoso and Adedire (2011) (40-45C), Ahmadi *et al*. (2012) (50 and 60 °C), Zibaee *et al*. (2012) (35-40 °C) Darvishzadeh and Bandani (2012) (50 °C) Darvishzadeh *et al*. (2013) (40 °C), Ahsaei *et al*. (2013) (45 °C); Sorkhabi-Abdolmaleki *et al*. (2014) (45 °C). Most of insect α-glucosidases are also mesophilic enzymes. They exhibit temperature optima values generally between 40 and 60 °C: Kouamé *et al*. (2005a) (50 °C), Wongchawalit *et al*. (2006) (40 °C), Ghadamyari *et al*. (2010) (45 °C), Sharifi *et al*. (2011) (60 °C), Aghaali *et al*. (2012) (50 °C), Riseh *et al*. (2012) (50 °C), Kaewmuangmoon *et al.* (2013) (45 °C).

As amylolytic enzymes, cellulolytic enzymes prospected within insects are generally mesophilic proteins. Many endoglucanases described in insects have displayed highest activity at 50 °C (Sami and Shakoori, 2008; Sajjadian *et al*., 2010; Sami *et al*., 2010; Willis *et al*., 2011; Sami *et al*., 2011) and 40-45 °C (Kim *et al*., 2008; Rehman *et al*., 2009, Hiroyama *et al*., 2010). Moreover, a few insect endoglucanases with temperatures optima of 60-65 ° C have been reported (Uddin *et al*., 2012; Bléi *et a*l., 2011; Hirayama *et al*., 2010; Tokuda *et al*., 1997). As for insect β-glucosidases, most of these glycosidases are optimally active in temperature range from 40 to 60 °C: Ferreira and Terra (1983) (40 °C); Pontoh and Low (2002) (50 °C); Kouamé *et al*. (2005b) (55 and 45 °C), Binaté *et al*. (2008) (45 °C), Xue *et al*. (2008) (40 °C), Yapi *et al*. (2009) (55 °C), Zhang *et al*. (2012) (49 °C), Ahsaei *et al*. (2013) (50 °C), Dehghanikhah *et al*. (2014) (50 °C) , Kouamé *et al*. (2005b) (55 and 45 °C).

In insect examined to date, the majority of xylanases are also mesophilic enzymes, although some reports indicate the existence of thermophilic xylanases in termite, particularly those obtained from the symbiotic fungus (Faulet *et al*., 2006a) (65-70 °C). Thus, reports indicate insect endoxylanases with temperature optima values of 37 °C (Padilla-Hurtado *et al*., 2012), 40 °C (Ratnadewi *et al*., 2007), 50 °C (Brennan *et al*., 2004; Héo *et al*., 2006 ; Sami *et al*., 2010); 55 °C (Roy *et al.,* 2003; Liu *et al*., 2011; Fagbohoun *et al*., 2012; Mattéoti *et al*., 2012), 60 °C (Faulet *et al.,* 2006b; Bléi *et al*.,2010). Regarding insect β-xylosidase, as pH, temperature effect is poorly investigated. However, a few reports indicate temperature optima value of 40 °C for β-xylosidase from digestive tract of termite *Coptotermes formosanus* (Azuma *et al*., 1984) and xylanolytic bacteria in the hindgut of beetle *Holotrichia parallela* larvae (Sheng *et al*., 2014).

Molecular weights: Insect amylolytic, cellulolytic and xylanolytic enzymes have been largely characterized in terms of molecular weights, except of β-xylosidase. Two methods are generally employed for estimating molecular weights of insect glycosidases: SDS-PAGE and gel filtration. Using each of these methods for estimating the molecular weight of the same enzyme may lead a small difference in the results. This small difference between the molecular weight determined by SDS-PAGE and by gel filtration could be explained by the specific interactions between the glycosyl residues of the enzymes and the gel filtration resin. Table 2 depicts molecular weigh values of some insect amylolytic, cellulolytic and xylanolytic enzymes.

Generally, molecular weights of insect α-amylases vary from about 26 to 89 kDa. Moreover, substantially all of the purified insect α-amylases were monomeric proteins. However, Kouadio *et al.* (2010b) have characterized two dimeric α-amylases from cricket *Gryllodes sigillatus* with molecular weights of 89 and 72 kDa by SDS-PAGE, then 85 and 66 kDa; by gel filtration. With regard to insect α-glucosidases, high molecular weight of 200 kDa has been found by gel filtration for one of the three isoforms of fruit fly *Drosophila melanogaster* α-glucosidases (Tanimura *et al*., 1979). By SDS-PAGE this isoform was a dimeric protein of two identical subunits of 93 KDa (Tanimura *et al*., 1979). As regard the two others isoforms, molecular weights have been estimated to 56 kDa by gel filtration, then 77 kDa by SDS-PAGE for one case, and 76 kDa by gel filtration, then 75 kDa by SDS-PAGE. Other reports have mentioned molecular weights indicated in table 2.

Regarding insect endoglucanases, as seen in table 2, the majority of reports devoted to their characterization in terms of molecular weight have focused on termites.

However, a few investigations have involved other insect orders. Moreover, interestingly, numerous of insect digestive endoglucanases exhibit several isoforms. This constitutes undoubtedly an avantage for the degradation of cellulose for herbivorous insects. As to insect β-glucosidases, their molecular weights estimation has involved several insect orders, including beetles, termites; honeybees and cockroaches. Apart from, β-glucosidases from *Erinnyis ello* (Santos and Terra, 1985), *Zygaena trifolii* (Franzi *et al*., 1989), *Macrotermes bellicosus* (Binaté *et al*., 2008) and *Nasutitermes takasagoensis* (Uchima *et al*., 2012), which had the relatively high molecular weights, majority of insect β-glucosidases molecular weights were in range of 45-95 kDa (Table 2).

With regard to xylanolytic enzymes, table 2 indicates that only the endoxylanases have been sufficiently characterized in terms of molecular weight. In addition, molecular weights of insect endoxylanase reported in literature, were overall relatively low compared to those of other insect glycosidases. For example, Matoub and Rouland (1995) have isolated three endoxylanases from the termite *Macrotermes bellicosus* and its symbiotic fungus *Termitomyces* sp. with molecular weights of 36, 56 and 22.5 kDa, determined by SDS-PAGE.

Table 2. Molecular weights and their determination method of some glycosidases from insect.

Insect species	Molecular weight and estimation method	References
α-amylase		
Morimus funereus (Coleoptera: Cerambycidae)	33 kDa by SDS-PAGE 31 kDa by Gel filtration	Dojnov *et al*. (2008)
Andralus spinidens (Hemiptera: Pentatomidae)	21.3 kDa by SDS-PAGE	Sorkhabi-Abdolmaleki *et al*. (2014)
Tenebrio molitor (Coleoptera:Tenebrionidae)	68 kDa by SDS-PAGE and by Gel fitration	Buonocore *et al*. (1976)
Sitophilus oryzae and *S. granarius* (Coleoptera: Curculionidae)	56 kDa by SDS-PAGE	Baker and Woo (1985)
Prostephanus truncatus (Coleoptera: Bostrichidae)	60.2 kDa by SDS-PAGE	Mendiola-Olaya *et al.* (2000)
Periplaneta americana (Blattodea: Blattidae)	60 kDa bySDS-PAGE 48 kDa by Gel filtration	Dué *et al*. (2008)
Antheraea mylitta (Lepidoptera: Saturniidae)	52 kDa by SDS-PAGE 50 kDa by gel filtration	Nagaraju and Abraham, (1995)
Bemisia tabaci (Aleyrodidae: Homoptera)	70 kDa by gel filtration	Cohen and Hendrix (1994)
Callosobruchus maculatus (Coleoptera: Bruchidae)	50 kDa by SDS-PAGE	Wisessing *et al*. (2008)
Rhyzopertha dominica (Coleoptera: Bostrichidae)	52 kDa by SDS-PAGE and by Gel filtration	Priya *et al.* (2010)
α-glucosidase		
Apis mellifera (Hymenoptera : Apidae)	98 kDa by SDS-PAGE (α-glucosidase I) 76 kDa by SDS-PAGE (α-glucosidase II) 68 kDa by SDS-PAGE (α-glucosidase III)	Takewaki *et al*. (1980) Nishimoto *et al*. (2001)
Acyrthosiphon pisum (Hemiptera: Aphididae)	72 kDa by SDS-PAGE	Cristofoletti *et al.* (2003)
Apis cerana japonica (Hymenoptera : Apidae)	82 kDa by SDS-PAGE	Wongchawalit *et al*. (2006)
Quesada gigas Hemiptera: Cicadidae)	61 kDa by SDS-PAGE	Fonseca *et al.* (2010)
Naranga aenescens (Lepidoptera: Noctuidae)	48 kDa by SDS-PAGE	Memarizadeh *et al.* (2014)

Rhynchophorus palmarum (Coleoptera: Curculionidae)	60.60 kDa by SDS-PAGE 61.05 kDa by Gel filtration	Yapi *et al.* (2015)
Endoglucanase		
Macrotermes mülleri (Isoptera: *Termitidae)*	34 kDa by SDS-PAGE (Cellulase I) 52 kDa by SDS-PAGE (Cellulase II)	Rouland *et al*. (1988)
Nasutitermes takasagoensis (Blattodea: *Termitidae)*	47 kDa by SDS-PAGE	Tokuda *et al*. (1997) Hirayama *et al.* (2010)
Reticulitermes speratus (Blattodea: Rhinotermitidae)	42 kDa by SDS-PAGE (YEG1) 41 kDa by SDS-PAGE (YEG2)	Watanabe *et al*. (1997)
Odontotermes formosanus (Isoptera: Termitidae)	80 kDa SDS-PAGE	Yang *et al.* (2004)
Coptotermes formosanus (Isoptera: Rhinotermitidae)	47 and 48 kDa by SDS-PAGE	Zhang *et al*. (2009)
Macrotermes subhyalinus (Isoptera:Termitidae)	63 kDa by Gel filtration (Cellulase C1) 27 kDa by Gel filtration (Cellulase C2)	Séa *et al.* (2006)
Ergates faber (Coleoptera: Cerambycidae)	25; 57 and 70 kDa by SDS-PAGE (Three isoforms)	Chararas *et al.* (1983)
Psacothea hilaris (Coleoptera: Cerambycidae)	47 kDa by SDS-PAGE	Sugimura *et al.* (2003)
Tribolium castaneum (Coleoptera: Tenebrionidae)	55 kDa by SDS-PAGE (Cel I) 35 kDa by SDS-PAGE (Cel II)	Rehman *et al*. (2009)
Mylabris pustulata (Coleoptera:Meloidae)	150 kDa by SDS-PAGE	Sami *et al.* (2011)
β-glucosidase		
Erinnyis ello (Lepidoptera: Sphingidae)	129 kDa by SDS-PAGE	Santos and Terra *(1985)*
Zygaena trifolii (Lepidoptera: Zygaenidae)	130 kDa by SDS-PAGE	Franzi *et al.*, (1989)
Macrotermes bellicosus (Isoptera: Termitidae)	204; 216 kDa by SDS-PAGE (Beta-Glc A) 209; 230 kDa by gel filtration (Beta-Glc B)	Binaté *et al.* (2008)
Nasutitermes takasagoensis (Blattodea: *Termitidae)*	169.5 kDa by gel filtration	Uchima *et al.* (2012)
Spodoptera frugiperda (Lepidoptera: Noctuidae)	47; 50 kDa by SDS-PAGE (Two isoforms)	Marana *et al*. (2000)
Neotermes koshunensis (Isoptera: Kalotermitidae)	60 kDa by SDS-PAGE 60 kDa by Gel filtration	Tokuda *et al*. (2002) Uchima *et al*. (2011)
Apis mellifera (Hymenoptera : Apidae)	72 kDa by SDS-PAGE	Pontoh and Low (2002)
Macrotermes subhyalinus (Isoptera:Termidae)	68 kDa by SDS-PAGE (Two isoforms)	Kouamé *et al.* (2005b)
Reticulitermes flaviceps (Blattodea: Rhinotermitidae)	93.6 kDa by SDS-PAGE	Xue *et al.,* (2008)
Rhynchophorus palmarum (Coleoptera: Curculionidae)	*58 kDa* by SDS-PAGE *60 KDa by gel filtration*	Yapi *et al.* (2009)
Endoxylanases		
Macrotermes bellicosus	36, 56 and 22.5 kDa by SDS-PAGE (Two	Matoub and Rouland (1995)

(Isoptera: Termitidae)	isoforms an one form from symbiotic fungus)	
Coptotermes formosanus (Isoptera: Rhinotermitidae)	19, 17 and 18 kDa by SDS-PAGE (Three isoforms)	Arakawa *et al.* (2009)
Samia cynthia pryeri (Lepidoptera: Saturniidae)	25 kDa by SDS-PAGE (form from bacteria of the insect intestine)	Roy *et al.* (2003)
Moechotypa diphysis (Coleoptera: Cerambycidae)	20 kDa by SDS-PAGE (form from bacteria from the insect digestive tract)	Heo *et al.* (2006)
Macrotermes subhyalinus (Isoptera: Termitidae)	60.1 kDa by SDS-PAGE 61.2 kDa by gel filtration	Faulet *et al.* (2006a)
Macrotermes subhyalinus (Isoptera: Termitidae)	87 kDa by SDS-PAGE (from symbiotic fungus) 80 kDa by gel filtration (the same form)	Faulet *et al*. (2006b)

Similarly, molecular weights of three endoxylanases from termite Coptotermes formosanus were below 20 kDa (Arakawa et al., 2009). Furthermore, an endoxylanase was purified in culture supernatant of xylanolytic bacteria from intestine of herbivorous insect *Samia cynthia* pryeri with low molecular weight (Roy *et al*., 2003). On the other hand, another endoxylanase was purified from culture supernatant of *Paenibacillus* sp. isolated from digestive tract of beetle *Moechotypa diphysis* with also low molecular weight (Heo *et al*., 2006), However, endoxylanases with slightly higher molecular weights were purified from termite *Macrotermes subhyalinus* and its symbiotic fungus (Faulet *et al.* 2006a; 2006b).

Effect of metal ions and chemical agents: One of the most important aspects in the characterization of insect glycosidases is effect of certain metal ions (generally Ca^{2+}, Fe^{2+}, Mg^{2+}, Na^{+}, Cu^{2+} and Zn^{2+}), Chelating agents such ethylenediaminetetraacetic acid (EDTA) and sulphydryl reagents such as 5,5-dithio-bis (2-nitrobenzoate) (DTNB) and *p*-chloromercurybenzoate (*p*CMB). About insect α-amylases, it is worth noting that most of the reports have shown activator effect of Ca^{2+} on these glycosidases like conventional microbial α-amylases, indicating that these are Ca^{2+}-dependent enzymes (Podoler and Applebaum, 1971; Buonocore *et al*., 1976; Cohen and Hendrix, 1994; Nagaraju and Abraham, 1995; Terra *et al.* 1996; Pelegrini *et al*., 2006; Dojnov *et al.,* 2008; Dué *et al*., 2008; Kouadio *et al*., 2010; Priya *et al*., 2010, Asadi *et al.,*2010; Darvishzadeh *et al*.,2013; Delkash-Roudsari *et al*., 2014; Sorkhabi-Abdolmaleki *et al.,* 2014). Indeed, Ca^{2+} is generally well known to be involved in maintaining stability of structure of α-amylases. However, there are a few insect α-amylases on which Ca^{2+} has an inhibitory effect (Mehrabadi and Bandani, 2009; Ahmadi *et al*., 2012; Ahsaei *et al*., 2013). Activities of certain insect α-glucosidases are also enhanced by addition of Ca^{2+} (Ghadamyari *et al*., 2010; Bandani *et al*., 2010). Concerning cellulolytic enzymes, it is noted that Ca^{2+} effect was poorly examined for insect endoglucanases and β-glucosidases. However, activator effect of Ca^{2+} on insect endoglucanases was reported for insects *Oxya chinensis* and *Leptinotarsa decemlineata* (Sami *et al*., 2010; Sajjadian *et al*., 2012). Moreover, inhibitor effect of Ca^{2+} has been described for β-glucosidase from insect *Leptinotarsa decemlineata* (Dehghanikhah *et al*., 2014). On the other hand, Ca^{2+} had no effect on β-glucosidases from termites *Macrotermes subhialinus* (Kouamé *et al*., 2005b); *Macrotermes bellicosus* (Binaté *et al.,* 2008); *Reticulitermes santonensis* (Mattéotti *et al*., 2011) and palm weevil *Rhynchophorus palmarum* (Yapi *et al.*, 2009). For xylanolytic enzymes, Ca^{2+} showed activator effect on endoxylanases from intestine of insect *Samia cyntia* pryeri (Roy *et al*., 2003); *Paenibacillus* sp. isolated from *Moechotypa diphysis* (Heo *et al*., 2006); termite *Macrotermes subhyalinus* worker (Faulet *et al*., 2006b) and soldier (Blei *et al*.,2010). Mg^{2+} has acted as an inhibitor of the activity of amylolytic, cellulolytic and xylanolytic enzymes from insects (Kouadio *et al*., 2010b; Ahmadi *et al*., 2012 ; Zibaee, 2013; Ahsaei *et al*., 2013; Shabarari *et al*., 2014; Dehghanikhah *et al*., 2014; Sorkhabi-Abdolmaleki *et al*., 2014), and in other cases as their activators (Kouamé *et al*., 2005b; Heo *et al*., 2006; Faulet *et al*., 2006b; Dué *et al.,* 2008; Asadi *et al*., 2010; Bandani *et al*., 2010; Priya *et a*l., 2010; Bléi *et al*., 2011; Zibaee *et al*., 2012; Sajjadian *et al.,* 2012; Darvishzadeh *et al*.,2013; Chitgar *et al.,* 2013). As to Mn^{2+}, it also acted as inhibitor on certain insect glycosidases (Heo *et al*., 2006; Xue *et al*., 2008; Asadi *et al*., 2010)) and as activator on others (Pelegrini *et al*., 2006; Faulet *et al*., 2006a; 2006b;

Uchima *et al*., 2012; Sorkhabi-Abdolmaleki *et al*., 2014). Others metal ions such as Fe^{2+}, Cu^{2+} and Zn^{2+} were, in general, inhibitors of these insect glycosidases (Kouamé *et al*., 2005b; Faulet *et al*. 2006a; Xue *et al*., 2008; Yapi *et al*., 2009; Asadi *et al*., 2010; Bléi *et al*., 2011; Uchima *et al*., 2012; Zibaee, 2013; Shabarari *et al.*, 2014; Sorkhabi-Abdolmaleki *et al*., 2014), although in a few cases, these ions were their activators (Asadi *et al*., 2010; Sorkhabi-Abdolmaleki *et al*., 2014). Effect of chelating agent EDTA has been also examined for insect glycosidases from several insect species. It was either inhibitor (Cohen and Hendrix, 1994; Cohen and Zeng, 2000b; Heo *et al*., 2006; Dué *et al.*, 2008; Priya *et al*., 2010; Asadi *et al*., 2010; Uchima *et al*., 2012; Ahsaei *et al*., 2013; Sorkhabi-Abdolmaleki *et al*., 2014) or activator (Asadi *et al*., 2010) or no effect (Xue *et al*., 2008; Bléi *et al*., 2011; Fagbohoun *et al.*, 2012). In addition, effects of sulfhydryl reagents such as DTNB and *p*CMB on number of insect glycosidases were also examined in order to know if sulfhydryl groups were essential in the catalysis of these enzymes. Thus, these reagents showed inhibitor effect on certain insect glycosidases, suggesting that sulfhydryl groups were essential for the catalytic action (Kouamé *et al*., 2005b; Faulet *et al*., 2006a; Binaté *et al*., 2008; Yapi *et al*., 2009; Bléi *et al*., 2011). But, these reagents had no effect on other insect glycosidases; thus indicating that sulfhydryl groups were not involved in the catalytic action (Blei *et al*., 2010; Fagbohoun *et al*., 2012).

Substrate specificity: In general, most of insect α-amylases displayed highest specificity towards starch, amylose, amylopectin and glycogen (Podoler and Applebaum, 1971; Buonocore *et al*., 1976; Cinco-Moroyoqui *et al*., 2008; Dué *et al*., 2008; Priya *et al*., 2010; Commin *et al*., 2013; Sorkhabi-Abdolmaleki *et al*., 2014). With regard to insect α-glucosidases, on the whole, they were characterized by the ability to hydrolyze any of phenyl-α-glucoside, maltose and sucrose (Tanimura *et al*., 1979; Takewaki *et al*., 1980 Nishimoto *et al*., 2001; Wongchawalit *et al*., 2006; Fonseca *et al*., 2010; Kaewmuangmoon *et al*., 2012). In addition, especially, α-glucosidase I from Japanese honeybee (*Apis cerana japonica*) exhibited hydrolytic activities toward maltooligosaccharides (maltotriose, maltotetraose and maltopentaose and kojibiose (having the α-1,2-glucosidic bond) (Wongchawalit *et al.*, 2006).

Generally, to test the substrate specificity of an endoglucanase, its activity against substrates such as CMC (Carboxymethylcellulose), avicel, filter paper and xylan was evaluated. Thus, endoglucanase from blister beetle *Mylabris pustulata* showed activity against CMC, avicel, filter paper and xylan (Sami *et al*., 2011). As to cellulase from termite *Coptotermes formosanus*, it degraded CMC, avicel and filter paper (Azuma *et al*., 1984). On the other hand, endoglucanases from termites (*Reticulitermes speratus* and *Nasutitermea takasago*ensis) displayed activities against CMC, HEC (Hydroxyethylcellulose) and insoluble cello-oligosaccharide (Hirayama *et al*., 2010). Several insect β-glucosidases displayed broad substrate specificity. Indeed, findings reported by several authors indicated that most of insect β-glucosidases were shown to have the polyspecificity between gluco-, fructo-, fuco-, galacto-xylo- based substrates (Ferreira and Terra, 1983; Marana *et al*. 2000; Ferreira *et al*. 2002; Kouamé *et al*. 2005b; Uchima *et al*., 2011). However, a few insect β-glucosidases were the exo-glycosidases with a high specificity for the β-glucosyl residue (Binaté *et al*., 2008; Yapi *et al*., 2009). Nevertheless, majority of these β-glucosidases had a high specificity toward the cellooligosaccharides up to four or even five units of glucose (Marana *et al*., 2000; Kouamé *et al*., 2005b; Ni *et al*., 2007; Binaté *et al*., 2008; Xue *et al*., 2008;Yapi *et al*., 2009). Moreover, oligosaccharides such as sophorose (having β-1,2-glucosidic bond), laminaribiose (having β-1,3-glucosidic bond), gentiobiose (having β-1,6-glucosidic bond) were sometimes, more or less hydrolyzed by insect β-glucosidases (Kouamé *et al*., 2005; Ni *et al*., 2007; Binaté *et al*., 2008; Xue *et al*., 2008; Yapi *et al*., 2009). Concerning insect endoxylanases, most of them displayed activity toward Beechwood xylan and Birchwood xylan (Matoub and Rouland, 1995; Faulet *et al*., 2006a; 2006b; Bléi *et a*l., 2010; Fagbohoun *et al*., 2012) or Birchwood xylan and spelt xylan (Roy *et al*., 2003). A few endoxylanases purified from insect showed a significant activity against CMC, indicating that these insect glycosidases were the bifunctional polysaccharidases (Faulet *et al*., 2006b; Bléi *et al*., 2010; Fagbohoun *et al*., 2012).

POTENTIAL APPLICATIONS

Due the similarities of some biochemical properties of insect amylolytic, cellulolytic and xylanolytic enzymes with those of conventional same enzymes from bacteria and fungi, many authors attempted to use the insect glycosidases in different applications. Evidently, the main potential application of insect α-amylases is their use as a target for the control of pest insects by

biotechnological strategies and development of novel biological and chemical α-amylases inhibitors (Bezerra *et al.*, 2014; Xu *et al.* 2014). This obviously concerns the amylases of insects which are major pest of crops, seeds and stored grains. Moreover, recent reports suggested the application of certain insect α-amylases in starch saccharification for the production of syrup of oligosaccharides mixture (Dué *et al*., 2008; Kouadio *et al.,* 2012). Moreover, Kouadio *et al*. (2012) reported that α-amylases from digestive tract of tropical house cricket *G. sigillatus* were able to catalyze the glycosylation of the phenolic compounds by transglycosylation reaction with starch as glycosyl donor. This constituted a valuable approach to improve the characteristics of these compounds such as solubility and stability for enhancing their usefulness as food and cosmetic ingredients. On the other hand, insect α and β-glucosidases were successfully tested in catalyzing of the synthesis of oligosaccharides and neoglycoconjugates by transglycosylation reaction (Kouamé *et al*., 2001; 2005a; 2005b; Yapi *et al*., 2009). Regarding insect cellulases, several recent reports have suggested their potential applications in plant biomass biodegradation for biofuel production (Willis *et al*., 2010; Oppert *et al*., 2010; Sun and Scharf, 2010; Adlakha *et al*., 2011; Haloi *et al*., 2011: 2012; Huang *et a*l., 2012; Upadhyaya *et al.*, 2012; Uddin *et al*., 2012; Vilanova *et al*., 2012; Su *et al*., 2013). As for insect xylanases, a few investigated enzymes have displayed biochemical properties that make them tools for use in biotechnological applications and in bio-bleaching in pulp and paper industry (Brennan *et al*., 2004; Faulet *et al.*, 2006a; 2006b; Liu *et al*., 2011) and also in lignocellulosic biomass conversion (Ni and Tokuda, 2013; Adlakha *et al*., 2011), like conventional microbial xylanases.

CONCLUSION

It emerges from this review that insect amylolytic, cellulolytic and xylanolytic enzymes are profusely distributed in insect kingdom. Indeed this review indicated that these insect digestive enzymes were successfully purified within several insect orders such as isoptera (termite), coleoptera (beetle), hymenoptera (honey bee), orthoptera (cricket,) and many others. Hence numerous reports were devoted to biochemical characterization including determination of optimum conditions, effects of chemical agents and metal ions and estimation of molecular weights. Regarding potential applications of these insect glycosidases, it follows from these reports that some of glycosidases may be targets which will allow developing new strategies of control of pests for stored grains and seeds whilst other could be used as tools in biotechnological and industrial applications.

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