PURIFICATION AND CHARACTERISATION OF RECOMBINANT XYLANASE FROM *Roseithermus sacchariphilus* STRAIN RA

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DEDICATION

Dedicated to my family and fellow friends

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ABSTRACT

Hemicellulases are important enzymes for applications in pulp and paper, animal feed, food and beverages, and biofuel industry. In the search for hemicellulases with promising properties, *Roseithermus sacchariphilus* strain RA could be a candidate source of enzymes. Strain RA is a Gram-negative halo-thermophilic bacteria isolated from a hot spring in Langkawi, Malaysia. Complete genome analysis revealed the bacterium encodes 57 glycoside hydrolases (GHs) that are affiliated to 30 GH families. Hemicellulases from GH 3, 10, and 43 are present in this bacterium. The objective of this project is to analyse an endo-xylanase (EC 3.2.1.8, GH10), designated as XynRA2. The XynRA2 gene consisted of 2,439 nucleotides encoding a protein with 813 amino acids. The protein sequence has the highest identity (98.6%) to the xylanase from *R. sacchariphilus* MEBiC09517^{T}. Three domains are present in XynRA2, namely (i) carbohydrate-binding module (CBM4_9), (ii) glycoside hydrolase family 10 (GH10) domain, and (iii) a C-terminal domain (CTD). In this study, two genes were cloned; native XynRA2 and its mutant, XynRA2ΔCBM, which lacked the CBM. The genes were cloned into the pET-28a(+) vector and expressed intracellularly in *E. coli* BL21 (DE3). The recombinant proteins carry a 6X-His-tag at both the termini were purified using Ni-NTA columns yielding proteins with weights of 89.5 kDa and 68.5 kDa, respectively. The enzyme activities were assessed using 3,5-dinitrosalicylic acid (DNS) assay against 1% (*w*/*v*) purified beechwood xylan. XynRA2 exhibited an optimum activity at 70°C and pH 8.5 in Tris-HCl buffer, with excellent activity (71%) in 5.0 M NaCl. On the other hand, XynRA2ΔCBM was most active at 70°C and pH 6.0 in acetate buffer although with a lower activity (54%) in 5.0 M NaCl. XynRA2 has a half-life of 45 min at 70°C but XynRA2ΔCBM has a shorter half-life (37 min). The specific activity and k_{cat} of XynRA2 were 300 U·mg^{-1} and 24.8 s^{-1}, whereas XynRA2ΔCBM were 160 U·mg^{-1} and 15.7 s^{-1}, respectively. Metal ions such as Na^{+}, K^{+}, and Ca^{2+} enhanced XynRA2 activity. Both XynRA2 and XynRA2ΔCBM hydrolysed exclusively xylose-based substrate including beechwood xylan and oat-spelt xylan. However, the product yield of XynRA2 on oat-spelt xylan was higher than XynRA2ΔCBM. The major end-products of hydrolysis by the enzymes were xylobiose (X_2) and xylotriose (X_3). Altogether, the results suggested removal of CBM affected the stability and activity of XynRA2. In summary, XynRA2 is an alkaline xylanase capable of withstanding high temperature and high NaCl concentration. These properties implied XynRA2 favours applications that require a combination of alkaline pH, high temperature, and the saline environment.

ABSTRAK

Hemiselulase ialah enzim penting untuk aplikasi dalam industri pulpa dan kertas, makanan haiwan, makanan dan minuman, dan biofuel. Dalam usaha mencari hemiselulase dengan ciri-ciri berpotensi, *Roseithermus sacchariphilus* strain RA didapati boleh menjadi sumber calon untuk enzim tersebut. Strain RA ialah bakteria halo-termofilik Gram-negatif yang dijumpai dari sebuah mata air panas di Langkawi, Malaysia. Analisis genom lengkap menunjukkan bakteria ini mengkod 57 hidrolase glikosida (GHs) yang berkaitan dengan 30 famili GH. Hemiselulase dari GH 3, 10, dan 43 didapati wujud dalam bakteria ini. Objektif projek ini adalah untuk menganalisa xilanase *endo* (EC 3.2.1.8, GH10) yang diberi nama sebagai XynRA2. Gen XynRA2 ini terdiri daripada 2,439 nukleotida yang mengekod untuk protein dengan 813 asid amino. Jujukan protein ini mempunyai identiti tertinggi (98.6%) dengan xilanase daripada *R. sacchariphilus* MEBiC09517^{T}. Tiga domin terdapat dalam XynRA2, iaitu (i) modul pengikatan karbohidrat (CBM4_9), (ii) domin famili hidrolase glikosida 10 (GH10), dan (iii) domin C-terminal (CTD). Dalam kajian ini, dua gen telah diklonkan, XynRA2 asal dan mutannya, XynRA2ΔCBM, tanpa CBM. Gen-gen protein ini diklon dalam vektor pET-28a (+) dan diekspres dalam sel *E. coli* BL21 (DE3). Protein rekombinan yang mempunyai 6X-His-tag pada kedua-dua terminal telah ditulenkan dengan turus Ni-NTA menghasilkan protein dengan berat molekul masing-masing sebanyak 89.5 kDa dan 68.5 kDa. Aktiviti enzim telah ditentukan dengan menggunakan cerakin asid 3,5-dinitrosalicylic (DNS) terhadap 1% (*w*/*v*) xilan *beechwood* tulen. XynRA2 menunjukkan aktiviti optimum pada suhu 70°C dan pH 8.5 dalam penimbal Tris-HCl, dengan aktiviti yang baik (71%) dalam 5.0 M NaCl. Sebaliknya, XynRA2ΔCBM adalah paling aktif pada suhu 70°C dan pH 6.0 dalam penimbal asetat, dengan aktiviti yang lebih rendah (54%) dalam 5.0 M NaCl. XynRA2 mempunyai separuh hayat selama 45 minit pada 70°C, manakala XynRA2ΔCBM mempunyai separuh hayat yang lebih pendek (37 minit). Aktiviti spesifik dan k_{cat} untuk XynRA2 adalah 300 U·mg^{-1} dan 24.8 s^{-1}, manakala untuk XynRA2ΔCBM adalah 160 U·mg^{-1} dan 15.7 s^{-1}. Ion-ion logam seperti Na^{+}, K^{+}, dan Ca^{2+} meningkatkan aktiviti XynRA2. Kedua-dua XynRA2 dan XynRA2ΔCBM menghidrolisa substrat yang berasaskan xilosa, seperti xilan daripada *beechwood* dan xilan daripada hampas gandum. Walau bagaimanapun, produk hasil oleh XynRA2 atas xilan hampas gandum adalah lebih tinggi daripada XynRA2ΔCBM. Produk utama daripada hidrolisis enzim-enzim ini adalah xilobiosa (X_2) dan xilotriosa (X_3). Hasil kajian ini mencadangkan ketiadaan CBM menjejaskan kestabilan dan aktiviti XynRA2. Secara ringkas, XynRA2 adalah xilanase alkali yang mampu menahan suhu tinggi dan kepekatan NaCl yang tinggi. Ciri-ciri enzim ini mengesyorkan kecenderungan XynRA2 bagi aplikasi-aplikasi yang memerlukan kombinasi pH beralkali, suhu yang tinggi, dan keadaan bergaram.

TABLE OF CONTENTS

LIST OF TABLE

LIST OF FIGURES

LIST OF ABBREVIATIONS

ANI	-	Average Nucleotide Identity
BCA	-	bicinchoninic acid
BSA	-	bovine serum albumin
BLASTp	-	Basic Local Alignment Search Tool for protein
CAZy	-	Carbohydrate-active Enzymes Database
CBM	-	carbohydrate-binding module
CMC	-	carboxymethylcellulose
CTD	-	C-terminal domain
DMSO	-	dimethyl sulfoxide
DNS	-	dinitrosalicylic acid
DTT	-	dithiothreitol
EDTA	-	ethylenediaminetetraacetic acid
ELSD	-	Evaporative Light Scattering Detector
GH	-	glycoside hydrolase
HPLC	-	High Performance Liquid Chromatography
IPTG	-	isopropyl β-D-1-thiogalactopyranoside
ITC	-	isothermal titration calorimetry
LB	-	Luria Bertani
MEGA 7	-	Molecular Evolutionary Genetics Analysis version 7
MWCO	-	molecular weight cut-off
NCBI	-	National Center for Biotechnology Information
Ni-NTA	-	nickel-nitrilotriacetic acid
OD_{600nm}	-	optical density at 600 nm
ORF	-	open reading frame
PorSS	-	Por secretion system
PDB	-	Protein Data Bank
SDS	-	sodium dodecyl sulfate
SDS-PAGE	-	sodium dodecyl sulfate polyacrylamide gel electrophoresis
TIM	-	triosephosphateisomerase
T9SS	-	type IX secretion system
XOs	-	xylo-oligosaccharides
X_1	-	xylose
X_2	-	xylobiose
X_3	-	xylotriose
X_4	-	xylotetraose
X_5	-	xylopentaose
X_6	-	xylohexaose

LIST OF SYMBOLS

α	-	alpha
β	-	beta
Å	-	angstrom
g	-	gravitational force
kDa	-	kilodalton
M	-	molar
pm	-	picometre
pKa	-	acid dissociation constant
p*I*	-	isoelectric point
rpm	-	round per minute
U	-	enzyme unit

LIST OF APPENDICES

CHAPTER 1

INTRODUCTION

1.1 Research background

Hemicellulose is the second most abundant structural material in plants. Hemicellulose often exists in the form of xylan, which comprises a backbone of β-1,4-linked xylopyranose with various side branches such as *O*-acetyl, α-4-*O*-glucuronic acid, α-L-arabinofuranose, *p*-coumaric acid, or ferulic acid at C-2 or C-3 positions (Collins, Gerday, and Feller, 2005). Beside xylan, hemicellulose comprises various types of polymeric sugars such as mannan, galactan and arabinan (Mathews, Pawlak, and Grunden, 2015). Owing to the complexity, complete hydrolysis of xylan requires synergism of various xylanolytic enzymes including endo-β-1,4-D-xylanase, β-D-xylosidase, α-D-glucuronidase, α-L-arabino-furanosidase, and acetylesterase (Moreira, 2016). Among these enzymes, endo-β-1,4-xylanase (also known as endo-β-xylanase, E.C. 3.2.1.8) plays a crucial role in hydrolysing the β-1,4-xylosidic bonds between two xylopyranose units in the xylan backbone to release short xylo-oligosaccharides (XOs).

According to the Carbohydrate-Active Enzyme (CAZy) database, endo-β-xylanases are currently grouped in glycoside hydrolases (GHs) families 5, 8, 10, 11, 30, 43, 51, 98, and 141. The majority of endo-β-xylanases belong to GH10 and GH11, which are distinctive of their respective origin, molecular properties and protein structure (Nguyen et al., 2018). Despite the variation among xylanases of different families, the protein architecture of xylanases comprises a catalytic domain which could sometimes be associated with one or more carbohydrate-binding modules (CBM) (Talamantes et al., 2016). Xylanases comprising only the catalytic domain (without the CBM) were also commonly reported (Chawachart et al., 2014; Evangelista et al., 2018; Niderhaus et al., 2018; Sharma et al., 2018). CBMs do not contribute to catalytic activity but function for recognition and binding to different

types of carbohydrates. With the presence of CBMs, enzymes could concentrate on the carbohydrate surface and improves the overall catalytic efficiency (Guillén, Sánchez, and Rodríguez-Sanoja, 2010). There are currently 85 families of CBMs, and these CBMs display considerable variation in substrate specificity against crystalline cellulose, non-crystalline cellulose, chitin, β-1,3/1,4-glucans, starch, glycogen, xylan, mannan, galactan, and inulin (Varnai et al., 2014). In the CAZy database, CBMs that are appended with GH10 xylanases were predominantly from families 1, 2, 3, 4, 6, 9, 13, 22 but fewer for families 10, 15, 35, and 37.

Xylanases are produced by a diverse group of organisms including bacteria, fungi, algae, protozoa, crustaceans, and insects (Chakdar et al., 2016). Fungal and bacterial xylanases are important due to their superior enzymatic properties, which might be applied in industrial processes (Chakdar et al., 2016). Xylanases have been used in a variety of applications. For instance, xylanases have been widely utilised for the delignification of paper pulp, modification of cereal food, improvement of digestibility of animal feedstock and production of xylo-oligosaccharides for pharmaceutical industries (Juturu and Wu, 2012). To collaborate better with these applications, many studies have been conducted to explore xylanases with various favourable properties. Thermostable alkaline xylanases are well-suited for bio-bleaching of pulp and paper (Kumar, Marín-Navarro, and Shukla, 2016), while thermostable acidic xylanases are applied in animal feed production (Luo et al., 2009). Xylanases that are active and stable in low pH or high pH values can be applied in hemicellulosic biomass saccharification (Chakdar et al., 2016). Xylanases having an optimum activity at low temperature and alkaline pH are introduced in the formulation of detergent as an additive (Kumar, Balakrishnan, and Rele, 2004). Earlier reports also proposed that xylanases obtained from psychrophilic microorganisms could be used to improve the quality of bread, fruit juices, and beer (Dornez et al., 2011; Nagar, Mittal, and Gupta, 2012). Halo-tolerant xylanases from halophilic might be used for wastewater treatment and processing of saline/salted food (Liu, Zhao, and Bai, 2013).

In the search for xylanase with promising properties, a rare halo-thermophilic bacterium could be a candidate source of enzyme. *Rhodothermaceae* strain RA (NCBI taxonomy ID: 1779382) is a bacterium isolated from a hot spring in Langkawi,

Malaysia (6°25'22.31"N, 99°48'48.97"E) (Goh et al., 2016). The bacterium exhibited similarity of 16S rDNA sequence (89.3%) and average nucleotide identity (ANI) value of 79.3 to the closest strain *Rhodothermus marinus* DSM 4252^T. This information suggests that *Rhodothermaceae* strain RA may represent a new genus in the family *Rhodothermaceae*. However, since polyphasic characterisations are yet to be determined, the bacterium was not officially proposed as a new taxa in taxonomic journals (such as International Journal of Systemic and Evolutionary Microbiology). Recently, in early 2019, Park et al. (2019) reported a strain MEBiC09517^T isolated from a port in South Korea. MEBiC09517^T was proposed as the first member of the new genus and the authors suggested that the strain was named *Roseithermus sacchariphilus* gen. nov., sp. nov. Due to high nucleotide similarity (ANI value of 96.2) between *Rhodothermaceae* strain RA and strain MEBiC09517^T, strain RA was proposed as a subspecies of *Roseithermus sacchariphilus*. To differentiate both strains, the bacterium was renamed *Roseithermus sacchariphilus* strain RA.

1.2 Problem statement

GHs are important enzymes that catalyse the hydrolysis of glycosidic bonds in polysaccharides to produce short oligosaccharides that have great industrial values. In the taxonomic family *Rhodothermaceae*, prominent GHs such as xylanase, cellulase, amylase and pullulanase, have been reported only for the bacterial species *R. marinus* (Halldórsdóttir et al., 1998; Karlsson et al., 1998b; Gomes, Gomes, and Steiner, 2003). So far, none of the proteins from *Roseithermus* have been cloned or characterised. The catalytic behaviour of the xylanase XynRA2 from *Roseithermus* is unknown. The similarities or differences between the xylanase from *Roseithermus* and the other well-characterised xylanases are yet to be determined. As the *R. sacchariphilus* strain RA was isolated from a saline hot spring, abiotic factors such as temperature and NaCl may have a consequence to the biochemical properties of XynRA2, however, this hypothesis has not been elucidated. Furthermore, the xylanase XynRA2 from *R. sacchariphilus* strain RA possesses a CBM and its function to the enzyme is yet to be discovered.

1.3 Research objectives

The objectives of this study are to:

1. Express and purify recombinant xylanase (XynRA2)
2. Determine the biochemical properties of recombinant XynRA2
3. Determine the effects of CBM removal to recombinant XynRA2

1.4 Scope of research

In order to achieve the objectives and provide an answer to the scientific problem statement mentioned earlier, the gene encoded for the xylanase (XynRA2) was cloned from the genome of *R. saccharіphilus* strain RA, and a mutation was performed by removing the CBM. The gene sequence of *xynRA2* (Genbank: ARA92359.1) was translated to protein sequence and was subsequently analysed using various bioinformatics software. Sequence alignment was performed to determine the sequence similarity with other closely related xylanases. The putative protein structure was predicted using homology modelling approach. The genes encoded for XynRA2 and its mutant XynRA2ΔCBM were expressed in *Escherichia coli* BL21 (DE3) cells. Both the recombinant XynRA2 and XynRA2ΔCBM were purified using affinity chromatography. The biochemical properties of XynRA2 and XynRA2ΔCBM were evaluated, and these properties include optimum catalytic pH and temperature, enzyme kinetics, substrate specificity, hydrolysis products, and the effects of NaCl, metal ions and chemical compounds to the enzyme activities.

1.5 Significance of research

Rhodothermaceae (thermophilic), *Rubricoccaceae* (mesophilic), *Salisaetaceae* (halophilic), and *Salinibacteraceae* (halophilic) are families of the order *Rhodothermales*. To date, this order consists of 10 genera, each of which has no more

than two species. The order is small, having only 15 validly described type strains. *Rhodothermus* spp. have been proven to produce important cellulosic and hemicellulosic hydrolases (Halldórsdóttir et al., 1998; Karlsson et al., 1998b; Gomes et al., 2003). However, none of the other genera in the order *Rhodothermales* have been studied for counterpart enzymes. As a new genus in this rarely studied order, xylanase from *Roseithermus* has not been characterised so far, therefore current study described for the first time the biochemical properties of a xylanase XynRA2 from *Roseithermus*. XynRA2 possesses a CBM. CBMs are responsible for carbohydrate recognition and binding (Varnai et al., 2014). To understand the role of CBM in the enzyme, a mutant XynRA2ΔCBM was constructed by removing the CBM from XynRA2. The findings elucidated from the protein-engineered xylanase contributes to the knowledge of the relationship between CBM and its appended enzyme. This is the first study on the GHs from the genus *Roseithermus*. Such study may address the feasibility of the xylanase and GHs from *Roseithermus* in future experiments, and probably the applications in carbohydrate saccharification.

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LIST OF PUBLICATIONS

1. **Teo, S. C.**, Liew, K. J., Shamsir, M. S., Chong, C. S., Bruce, N. C., Chan, K. G., & Goh, K. M. (2019). Characterizing a halo-tolerant GH10 xylanase from *Roseithermus sacchariphilus* strain RA and its CBM-truncated variant. *International Journal of Molecular Sciences*, *20*(9), 2284. https://doi.org/10.3390/ijms20092284 **(Q2, IF: 4.183)**