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FUNCTIONAL CHARACTERIZATION OF ALCOHOL DEHYDROGENASE GENES IN ARABIDOPSIS PLANTS GROWN UNDER DROUGHT CONDITION

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By

THAWDA MYINT

Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in Fulfilment of the Requirement for the Degree of Doctor of Philosophy

June, 2013

DEDICATED TO;

MY BELOVED PARENTS

Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfilment of the requirement for the degree of Doctor of Philosophy

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Chairman: **Assoc. Professor Mohd Puad Abdullah, PhD**

Faculty: **Biotechnology and Biomolecular Sciences**

In response to drought, plants change their metabolic activities towards limiting cellular water consumption and loss. One metabolic process that is affected by this stress is ethanolic fermentation. In plants, ethanolic fermentation occurs during limited oxygen condition and under certain environmental stresses. The effects of ethanol fermentation on plant growth and survival under drought stress are not well explained. In addition, previous studies on ethanolic fermentation in plants were limited to alcohol dehydrogense (EC.1.1.1.1) enzyme activity and gene expression. In this study, it was hypothesized that ethanolic fermentation is required to enhance plant ability to retain cellular water under drought. Enhancing the capacity of ethanolic fermentation in a plant would improve the plant ability to retain cellular water; thus, retain the plant's photosynthetic capacity. To test the hypothesis, this study was carried out with the following objectives: i) to identify the specific *ADH* genes responding to drought in *Arabidopsis* plants, ii) to evaluate the effects of defective *ADH* on growth and drought-related parameters, iii) to evaluate the effects of enhanced ethanolic fermentation on growth and drought-related parameters. The objectives were achieved by a combination of the gain-and the loss-of-function approaches. For the gain-of-function approach, an *Arabidopsis* plant over-expressing the *ADH1* transgene was developed using the Gateway technology where fully characterized homozygous lines were used for the analysis. As for the loss-of-function approach, the T-DNA insertion mutant lines with impaired *ADH* genes were used. The plants were exposed to polyethylene glycol-induced drought stress, and their responses at physiological, biochemical and molecular levels were analysed together with their overall growth performance.

In the present study, the level of relative water content (RWC) of *Arabidopsis* plants dropped to 75% from the initial level of 85% when treated with 5% (w/v) PEG-20,000, demonstrated that the plants were moderately water-stressed. The stressed plants had high levels of proline and low levels of chlorophyll. At enzyme and metabolite levels, both the root and leaf NADH-ADH activities were increased 5.9 and 4.4 folds, respectively. For pyruvate decarboxylase (PDC), the activity was increased in the root

(1.2 folds) and in the leaf (4.4 folds). Ethanol, the end product of ethanol fermentation was accumulated in both the leaf (3 folds) and root (2 folds). The increase in the level of ethanol was parallel with the increase observed in the activities of NADH-ADH and PDC. At gene level, the majority of the *ADH* and *PDC* genes were up-regulated. Two of the *PDC* genes (*AT5G01320* and *AT4G33070*) genes and three of the *ADH* genes (*AT1G64710*, *AT1G77120* and *AT5G24760*) were up-regulated in the leaf and root. These evidences support the conclusion that the capacity of ethanolic fermentation was enhanced in response to drought.

When the individual *ADH* gene was defective, a severe reduction in the ADH activities and growth performance of the mutant plants were observed when exposed to drought. The T-DNA insertion *adh* knock-out mutant lines [*adh1*mutant (AT1G77120) and two *adh-like* mutants (AT1G64710 and AT5G24760)] demonstrated reduced growth judging by a shorter root system and lower biomass content. The plants also failed to retain cellular water which subsequently affected their physiological process including photosynthesis.

In the transgenic *Arabidopsis* plant over-expressing the *ADH1* gene, the capacity of ethanolic fermentation was enhanced judging by the increase in the ADH enzyme activity (6 folds). Under drought stress, the transgenic plant exhibited the following phenotypic improvements i) improved ability to retain cellular water; ii) increased chlorophyll content; iii) increased proline level; iv) increased NADH-ADH activity; v) increased volume of root system and iv) increased biomass. All these features contributed to the overall improvement of the transgenic plants under drought.

As a conclusion, ethanolic fermentation is important for plants grown under drought condition. Enhancing the capacity of ethanolic fermentation improves plant ability to maintain cellular water; thus, supports the normal function of photosynthesis. To reduce the impacts of drought in plants, the capacity of plant ethanolic fermentation may be enhanced, and this strategy could be implemented in crop plants of economic importance.

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PENCIRIAN FUNGSI GEN ALKOHOL DEHIDROGENASE DALAM TUMBUHAN ARABIDOPSIS DI BAWAH KEADAAN KEMARAU

Oleh

THAWDA MYINT

Jun, 2013

Pengerusi: Profesor Madya Mohd Puad Abdullah, PhD

Fakulti: Bioteknologi dan Sains Biomolekul

Sebagai tindak balas kepada kemarau, tumbuhan mengubah aktiviti metabolisme ke arah penjimatan penggunaan dan kehilangan air. Satu proses metabolisme yang dipengaruhi oleh stres ini adalah fermentasi etanol. Dalam tumbuhan, fermentasi etanol berlaku semasa keadaan kekurangan oksigen dan di bawah stres alam sekitar yang tertentu. Kesan fermentasi etanol ke atas pertumbuhan tumbuhan yang hidup dalam keadaan kemarau tidak diketahui dengan jelas. Di samping itu, kajian terdahulu mengenai fermentasi etanol dalam tumbuhan terbatas kepada aktiviti enzim dan gen alkohol dehidrogense (EC.1.1.1.1). Hipotesis kajian ini adalah fermentasi etanol diperlukan untuk meningkatkan keupayaan tumbuhan untuk mengekalkan air sel dalam keadaan kemarau. Meningkatkan kapasiti fermentasi etanol akan meningkatkan keupayaan tumbuhan untuk mengekalkan air sel; oleh itu, mengekalkan kapasiti fotosintesis. Untuk menguji hipotesis tersebut, kajian ini dijalankan dengan objektif berikut: i) untuk mengenal pasti gen *ADH* tertentu yang bertindakbalas ke atas kemarau dalam tumbuhan Arabidopsis, ii) untuk menilai kesan kecacatan gen *ADH* kepada pertumbuhan dan parameter kemarau yang berkaitan, iii) menilai kesan peningkatan kapasiti fermentasi etanol ke atas pertumbuhan dan parameter kemarau yang berkaitan. Objektif berkenaan telah dicapai melalui pendekatan kehilangan-fungsi dan kedapatan-fungsi gen *ADH*. Bagi pendekatan kedapatan-fungsi, tumbuhan Arabidopsis yang mengekspreskan *ADH1* secara berlebihan telah dibangunkan menggunakan teknologi Gateway. Pokok homozigous yang telah dicirikan sepenuhnya telah digunakan untuk tujuan analisis. Bagi pendekatan kehilangan-fungsi, tumbuhan arabidopsis mutan yang mempunyai selitan T-DNA dengan gen *ADH* yang cacat telah digunakan. Tumbuhan tersebut telah didedahkan kepada polietilena glikol untuk menjana kesan stres kemarau, dan tindak balas tumbuhan tersebut di peringkat fisiologi, biokimia dan molekul telah dianalisis bersama dengan prestasi pertumbuhan tersebut secara keseluruhan.

Dalam kajian ini, tahap kandungan air relatif (RWC) tumbuhan Arabidopsis menurun kepada 75% daripada tahap awal sebanyak 85% apabila dirawat dengan 5% (w / v) PEG-20, 000, menunjukkan bahawa tumbuhan tersebut berada di bawah stres kemarau yang sederhana. Tumbuhan tersebut mempunyai tahap prolina yang tinggi

dan paras klorofil yang rendah. Pada peringkat enzim dan metabolit, aktiviti enzim NADH-ADH pada akar dan daun telah meningkat sebanyak 5.9 dan 4.4 kali ganda, masing-masing. Manakala untuk enzim piruvat dekarboksilase (PDC), aktiviti enzim tersebut telah meningkat pada akar (1.2 kali ganda) dan daun (4.4 kali ganda). Etanol, produk akhir fermentasi etanol telah terkumpul di dalam daun (3 kali ganda) dan akar (2 kali ganda). Peningkatan paras etanol adalah selari dengan peningkatan yang diperhatikan dalam aktiviti enzim NADH-ADH dan PDC. Di peringkat gen, majoriti gen *ADH* dan *PDC* telah meningkat dengan ketara. Dua daripada gen *PDC* (AT5G01320 dan AT4G33070) dan tiga daripada gen *ADH* (AT1G64710, AT1G77120 dan AT5G24760) telah mengalami kenaikan dalam pengekspresan yang ketara pada daun dan akar. Kesemua bukti berkenaan menyokong peningkatan kapasiti fermentasi etanol sebagai tindak balas terhadap kemarau.

Apabila gen *ADH* mengalami kecacatan, pengurangan yang ketara dalam aktiviti enzim ADH dan prestasi pertumbuhan tanaman mutan telah diperhatikan apabila tumbuhan tersebut didedahkan kepada kemarau. Tumbuhan mutan Arabidopsis yang mempunyai selitan T-DNA dengan gen *ADH* yang cacat [mutan *adh1* (AT1G77120) dan dua mutan *adh*-setara (AT1G64710 dan AT5G24760)] telah menunjukkan penurunan dalam prestasi pertumbuhan berdasarkan kepada sistem akar yang pendek dan biomas yang rendah. Tumbuhan tersebut juga gagal untuk mengekalkan air sel dan seterusnya telah menjejaskan proses fisiologi termasuk fotosintesis.

Dalam tumbuhan Arabidopsis transgenik yang mengekspreskan gen *ADH1* secara berlebihan, kapasiti fermentasi etanol telah dipertingkatkan berdasarkan kepada peningkatan aktiviti enzim ADH (6 kali ganda). Di bawah stres kemarau, tumbuhan transgenik tersebut mempamerkan penembahbaikan fenotip seperti berikut: i) peningkatan keupayaan untuk mengekalkan air sel; ii) peningkatan kandungan klorofil; iii) peningkatan paras prolina; iv) peningkatan aktiviti enzim NADH-ADH; v) peningkatan jumlah akar; dan iv) peningkatan biomas. Ke semua ciri-ciri ini menyumbang kepada peningkatan prestasi keseluruhan tumbuhan transgenik tersebut di bawah keadaan kemarau.

Kesimpulannya, fermentasi etanol adalah penting untuk tumbuhan di bawah keadaan kemarau. Meningkatkan kapasiti fermentasi etanol telah meningkatkan keupayaan tumbuhan untuk mengekalkan air sel; oleh itu, menyokong fungsi normal fotosintesis. Untuk mengurangkan kesan kemarau pada tumbuhan, kapasiti fermentasi etanol dalam tumbuhan boleh dipertingkatkan dan strategi ini boleh dikembangkan kepada tanaman yang mempunyai kepentingan ekonomi.

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I certify that an Examination Committee has met on .... to conduct the final examination of THAWDA MYINT on her thesis entitled "Functional Characterization of Alcohol dehydrogenase Genes in *Arabidopsis* Plants Grown Under Drought Condition''in accordance with the Universities and University College Act 1971 and the Constitution of the Universiti Putra Malaysia [P.U.(A) 106] 15 March 1998 The Committee recommends that the student be awarded the Doctor of Philosophy.

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µg	microgram
µl	microliter
µM	micromolar
%	percentage
ACS	acetyl-CoA synthetase
ADH	alcohol dehydrogenase
ALDH	aldehyde dehydrogenase
ANOVA	analysis of variance
ATP	adenosine-5'-triphosphate
BLAST	basic local alignment search tool
bp	base pair
BSA	bovine serum albumin
CaMV	cauliflower mosaic virus
cDNA	complementary DNA
Chl	chlorophyll
CTAB	cetyltrimethylammonium bromide
C-terminal	carboxyl terminal
DEPC	Diethylpyrocarbonate
DNA	deoxyribonucleic acid
dNTPs	mixture of dATP, dTTP, dCTP and dGTP
DTT	dithiothreitol
DW	dry weight
EDTA	ethylenediaminetetraacetic acid
gfp	green fluorescent protein
g	gram
gus	β-glucuronidase
g/L	gram per liter
H_2O_2	hydrogen peroxide
H_3PO_4	Phosphoric acid
hptII	hygromycin phosphotransferase II
$K_3Fe(CN)_6$	Potassium ferricyanide
$K_4Fe(CN)_6$	Potassium ferrocyanide
kbp	kilo-base pair
KCl	Potassium Chloride
L	liter
LB	Lysogeny broth
LDH	lactate dehydrogenase
LEA	Late Embryogenesis abundant
M	molar
Mb	mega bases
MCS	multiple cloning sites
$MgCl_2$	Magnesium Chloride
$MgSO_4$	Magnesium Sulphate
min	minute
ml	milliliter
mm	millimeter
mM	millimolar
Mpa	Megapascal (water potential unit)

mRNA	messenger ribonuleic acid
MS	medium of Murashige and Skoog
Na_3PO_4	sodium phosphate
NAD	nicotinamide adenine dinucleotide
NADP	nicotinamide adenine dinucleotide phosphate
NCBI	national center for biotechnology information
ng	nanogram
NH_4	ammonium
nm	nanometer
NO_3^-	nitrate
npt-II	neomycin phosphotransferaseII
OD	optical density
OH	hydroxide
ORF	open reading frames
P5CS	Δ 1 -pyrroline-5-carboxylate synthetase
PCR	polymerase chain reaction
PDC	pyruvate decarboxylase
PDH	pyruvate decarboxylase dehydrogenase
pg	pictogram
PEG	Polytheylene glycol
PVP-40	polyvinylpyrrolidone
RNA	ribonuleic acid
RNase	ribonulease
ROS	reactive oxygen species
rpm	rotation per minute
RT	room temperature
RT-PCR	Reverse transcriptase polymerase chain reaction
RuBP	Ribulose-1,5-bipohosphate
RWC	Relative water content
SDS	sodium dodecyl sulphate
SE	standard error
s	second
SOD	superoxide dismutases
TAE	Tris-acetate-EDTA
TCA	tri carboxylase acid
Tm	melting temperature
TW	turgid weight
U	Unit
UTR	untranslated region
UV	Ultra violet
V	volt
v/v	volume per volume
w/v	weight per volume
X-Gluc	5-bromo-4-chloro-3-indolyl-β-D-glucuronide

CHAPTER 1

INTRODUCTION

The impacts of global warming and climate change are becoming important. Especially in prolonged drought and frequent flooding are common phenomenon in many parts of the world (Qiu, 2010; Schiermeier, 2011). Together with other biotic and abiotic stresses including salinity, low temperature, pest and disease, these could severely affect agricultural productivity as the stress could restrict the expression of the full genetic potential of a crop plant, and threaten the sustainability of agricultural industry (Shilpi and Narendra, 2005). One estimate puts a reduction of more than 50% in yield because of environmental stress (Bray, 2000).

Drought severely reduces plant productivity as a result of reduced photosynthetic capacity (Hummel *et al.,* 2010) through stomatal closure of CO_2 diffusion (Sharkey, 1990; Chaves, 1991; Ort*et al*., 1994; Cornic and Massacci, 1996) or by metabolic impairment of carbon reduction cycle (Boyer, 1976; Lawlor, 1995; Allen and Ort, 2001). Evidence that impaired ATP synthesis is the main factor limiting photosynthesis even under mild drought (Boyer, 1976; Tezara *et al*., 1999) has further stimulated debate (Cornic, 2000; Lawlor and Cornic, 2002). While some plants can withstand the adverse effects of prolonged drought, most are not able to hold their metabolic function long enough for survival before the rain fall again. The mechanism that governs these differential abilities of different plants to withstand different intensities of drought is not fully understood. Changes in the levels of certain metabolites such as chlorophyll content, sugar-alcohol and proline are commonly observed in the plants exposed to drought condition (Sperdouli and Moustakas, 2012; Silvente *et al*., 2012); however, these biochemical changes are often overlapped with plant responses to other environmental stresses.

To overcome this potential threat to agriculture, scientists turn to biotechnology for long-term solution of intensifying research on various aspects of plant adaptative response and survival to various environmental stresses. One approach is to utilize genome-wide expression analysis where drought-related genes could be obtained from thousands of genes analysed (Seki *et al*., 2002, Patrica *et al*., 2011). The efforts were proven to be fruitful as scientists can identify important genes related to drought and carry out gene functional studies for more in-depth analysis of drought gene network.

One particular gene that responds to drought is alcohol dehydrogenase (*ADH*). In *Arabidopsis* plant, alcohol dehydrogenase enzyme (EC.1.1.1.1) has been encoded by *ADH* gene which is involved in mediating stress responses, mainly in anaerobic condition (Dolferus *et al.,* 1994; Peters and Frenkel, 2004). In addition, numerous stress-induced genes have been identified using microarray experiment in which *ADH* gene was up-regulated under drought condition (Seki *et al.,* 2002). This observation supports an earlier study on ethanol production under drought condition. Kimmerer and Kozolowski (1982) reported that high level of ethanol content was produced in dehydrated woody plants. These evidences of upregulation of *ADH* gene expression and production of ethanol under drought condition connect to induction of ethanolic fermentation as ADH is the main enzyme of ethanolic fermentation. So far, little effort has been done in experiments to follow up these findings with functional studies of the *ADH* gene in plants exposed to drought stress condition.

Ethanolic fermentative pathway normally occurs in plants grown under anaerobic condition. This topic has been well researched in animals and yeasts but not so much in plants. Under hypoxic conditions where molecular oxygen becomes limited, fermentative enzymes in the ethanolic pathway are upregulated, causing increased production of ethanol and NAD^+. The cofactor NAD^+ was generated as a by-product of this process is what makes ethanolic fermentation important for the survival of living systems under anaerobic condition. In the context of the fermentative enzyme in plants, the activities of the ADH enzymes are up-regulated not only in anaerobic conditions but also in other environmental stresses condition where oxygen was not completely depleted (Robert *et al*., 1984; 1989; Tadege *et al*., 1998; Mustroph and Albrecht, 2003; Geigenberger, 2003; Fukao and Bailey-Serres, 2004). Hence, some suggest that plant ADH (EC.1.1.1.1) is involved in stress adaptation mechanism for energy production (Tesniere *et al.,* 2006; Ismond *et al*., 2003; Kato-Noguchi *et al*., 2006).

Previous functional analyses of the *ADH* gene were mainly done on the effects of the over-expression on plant tolerance to low oxygen levels when the plant or cells are submerged in water (Shiao *et al*., 2002, Ismond *et al.,* 2003). In the model plant, *Arabidopsis thaliana*, the ADH enzyme (EC 1.1.1.1) is encoded by the *ADH1* gene and other seven *ADH*-like genes (The Arabidopsis Genome Initiative, 2000). So far, only *ADH1* has been studied in the plant including its expression. The gene was reported to be associated with various environmental stresses. However, the mechanism of alcohol dehydrogenase genes *(ADH)* function under drought stress is still not clear.

In this study, it was hypothesized that ethanolic fermentation is required to enhance plant ability to retain cellular water under drought stress condition. Enhancing ethanolic fermentation in a plant would improve water retention in the plant; thus, improving the plant photosynthetic capacity. The hypothesis was tested in a combination of the gain- or loss-of-function approaches. For the gain-of-function approach, an *Arabidopsi*s plant overexpressing the *ADH1* transgene was developed using the Gateway technology; fully characterized homozygous lines were used for the analysis. As for the loss-of-function approach, the T-DNA insertion mutant lines with impaired *ADH* genes were used. The plants were exposed to PEG-induced drought stress conditions, and their responses at the physiological, biochemical and molecular levels were analysed together with their overall growth performance.

To test the hypothesis, this study was carried out with the following objectives:

i) to identify the specific *ADH* genes in *Arabidopsis thaliana* responding to drought stress condition
ii) to evaluate the impacts of defective *ADH* on growth and drought-related parameters of plant
iii) to evaluate the impacts of enhanced ethanolic fermentation on growth and drought-related parameters

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