Contents lists available at ScienceDirect



Review

Environmental and Experimental Botany





Role of ethylene and the APETALA 2/ethylene response factor superfamily in rice under various abiotic and biotic stress conditions



Rambod Abiri^{a,b}, Noor Azmi Shaharuddin^{a,d,*}, Mahmood Maziah^{a,c,d,*}, Zetty Norhana Balia Yusof^a, Narges Atabaki^e, Mahbod Sahebi^d, Alireza Valdiani^a, Nahid Kalhori^f, Parisa Azizi^d, Mohamed M. Hanafi^d

^a Department of Biochemistry, Faculty of Biotechnology and Bimolecular Sciences, Universiti Putra Malaysia, 43400, UPM Serdang, Selangor DE, Malaysia

^b Young Researchers and Elite Club of IAU, Kermanshah, Iran

^c Institute of Bioscience, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor DE, Malaysia

^d Institute of Tropical Agriculture, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor DE, Malaysia

^e IAU of Tehran Science and Research Branch, Tehran, Iran

^fDepartment of Biology, Faculty of Science, University Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

ARTICLE INFO

Article history: Received 29 September 2016 Received in revised form 29 October 2016 Accepted 29 October 2016 Available online 31 October 2016

Keywords: Ethylene Transcription factor AP2/ERF Stress Rice

ABSTRACT

Ethylene, the simplest gaseous plant growth regulator (PGR), controls diverse physiological pathways in plants. Under various stress conditions and during different developmental stages, such as root elongation, leaf and flower senescence, seed germination, tissue differentiation and organ abscission, ethylene biosynthesis is significantly increased. In rice, the internal ethylene concentration is rapidly regulated to a genetically, physiologically and morphologically relevant level under various stresses. Regulation of the ethylene signalling pathway under adverse conditions results in up- and/or downregulation of the expression of stress-related genes in different families. Transcription factors are proteins that influence and control a number of biological processes under both normal and stress conditions. APETALA 2/ethylene response factor (AP2/ERF) is a transcription factor that is considered to function in stress response pathways in rice. To date, many AP2/ERF genes have been functionally characterised in rice. An understanding of the interactions between the AP2/ERF genes and ethylenedependent mechanisms may provide new insights to facilitate the enhanced adaptation of rice to stress. In the current review, the structure and function of ethylene in rice under normal and stress conditions are described, and then the general functions of the plant AP2/ERF transcription factors are discussed. In addition, the interactions between the AP2/ERF genes and ethylene pathways under abiotic stresses, including submergence, cold, salinity, drought and heavy metal stresses, as well as those under biotic stresses, are summarised. Although the AP2/ERF genes have been identified, information on the physiological mechanisms of this gene family under stress conditions in rice remains limited. Therefore, further physiological studies must be performed in the future to identify additional features of this crucial gene family.

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E-mail addresses: rambod_abiri@yahoo.com (R. Abiri), noorazmi@upm.edu.my (N.A. Shaharuddin), maziah.mahmood@gmail.com (M. Maziah).

http://dx.doi.org/10.1016/j.envexpbot.2016.10.015

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^{*} Corresponding authors at: Department of Biochemistry, Faculty of Biotechnology and Biomolecular Sciences, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor DE, Malaysia.

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1. Introduction

Ethylene (ET) is a gaseous phytohormone involved in various processes that are required for plant germination, growth and development (Ju and Chang, 2015; Schaller and Voesenek, 2015). This phytohormone either induces or inhibits its own synthesis in a process termed "autoinduction" or "autoinhibition", respectively (Donnell et al., 1996). At an optimum concentration and with appropriate timing, the application of ET promotes agricultural production by enhancing the growth of treated crops. In addition, the combined application of ET with other hormones, such as cytokinin and auxin, allows for regulation of the ethylene level and further enhances agricultural production (Müller and Munné-Bosch, 2011; Bakshi et al., 2015). Further, the application of ethylene to field decreases production cost considerably as it reduces the fruit removal force, which can diminish the damage rate during mechanical harvesting. This gaseous hormone can be applied to a wide variety of plants for manipulation of harvesting during the daytime (Cohen and Kende, 1986). It has also been reported to regulate plant biological mechanisms in response to various abiotic (submergence, drought, salt, flooding, and cold) and biotic (insect, fungal, and microbial infections) stresses (Donnell et al., 1996; Broekaert et al., 2006; Van Loon et al., 2006; Grennan, 2008; Müller and Munné-Bosch, 2015). Depending on the adverse conditions, it acts as either a positive or negative modulator (Yoo et al., 2009).

In rice, the ethylene signalling cascade involves a variety of transcription factor families. The regulation of stress-responsive genes by transcriptional regulatory factors, also known as transcriptome reprogramming, is a critical step in the development of rice responses to a wide spectrum of environmental stresses. To date, multiple regulatory transcription factors that are necessary for transcriptome reprogramming under detrimental conditions have been identified and functionally analysed. These transcription factors have been classified into various superfamilies, and the APETALA 2/ethylene-responsive element binding factor (AP2/ERF) superfamily is one of the largest transcription factor superfamilies in crops (Singh et al., 2002). The interactions between ethylene and this superfamily may play significant roles in the regulation of physiological processes

under normal and detrimental conditions (Müller and Munné-Bosch, 2015). Therefore, functional evaluation of the ethylene signalling network that involves the AP2/ERF superfamily may facilitate the determination of how ethylene modulates adaptive stress responses in plant (Rzewuski and Sauter, 2008). Previous investigations on the ethylene and AP2/ERFs role under diverse conditions have mainly focused on dicotyledonous plants such as *Arabidopsis*, tobacco and tomato. However, relevant studies in monocotyledonous species, such as rice have not been systematically summarised. To the best of our knowledge, this is the first report on some intriguing aspects of ethylene interaction with AP2/ERF family members related to adaptive responses of rice to different environmental conditions.

2. Physio-molecular pathway of ethylene biosynthesis in rice

S-adenosylmethionine (AdoMet) is a primary amino acid component of the ethylene biosynthesis pathway. In the first committed step of ethylene biosynthesis in rice, AdoMet is converted into 1-carboxylic acid (ACC) and a by-product, 50methylthioadenosine, in a reaction catalysed by 1-amino-cyclopropane-1-carboxylic acid (ACC) synthase (ACS) (Fig. 1) (Rzewuski and Sauter, 2008). ACS belongs to a family of proteins (PLPdependent enzymes) that require a cofactor (pyridoxal-5'-phosphate). This enzyme catalyses elimination, carboxylation, deamination, transamination or replacement of the γ and β carbons of amino acids (Argueso et al., 2007). ACS is induced by various developmental and environmental factors via different gene families in rice (Yamagami et al., 2003; Tsuchisaka and Theologis, 2004). Based on their C-termini, three types of ACS proteins regulated by a small multigenic family have been identified in rice (Iwai et al., 2006). Type-1 ACS proteins have the longest C-termini and contain a conserved Ser that is a phosphorylation site for calcium-dependent protein kinase (CDPK), in addition to three Ser residues that are potentially phosphorylated by the mitogenactivated protein kinase MPK6 (Tatsuki and Mori, 2001; Sebastià et al., 2004). In addition, type-2 ACS proteins include the Ser phosphorylation site for CDPK, and type-3 ACS proteins possess the shortest C-termini and lack phosphorylation sites (Rzewuski and Sauter, 2008).



Fig. 1. The ethylene biosynthetic pathway in rice. The enzymes that catalyse each step are shown under the arrows. AdoMet: AdoMet synthetase produces AdoMet at the expense of ATP; Met: methionine; ACC: 1-aminocyclopropane-1-carboxylic acid; and MTA: methylthioadenine. MTA is recycled back to methionine through the Yang cycle, successively involving MTA nucleosidase. ACC and MTA are released in each reaction (Argueso et al., 2007).

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