Available online at www.sciencedirect.com

ScienceDirect

Plant Physiology and Biochemistry 44 (2006) 261–273

Plant Physiology and Biochemistry

www.elsevier.com/locate/plaphy

Review article

Role of defense/stress-related marker genes, proteins and secondary metabolites in defining rice self-defense mechanisms

Nam-Soo Jwa[a], Ganesh Kumar Agrawal[b,1], Shigeru Tamogami[c], Masami Yonekura[d], Oksoo Han[e], Hitoshi Iwahashi[f], Randeep Rakwal[b,f,*]

[a] *Department of Molecular Biology, College of Natural Science, Sejong University, Seoul 143-747, Republic of Korea*
[b] *Research Laboratory for Agricultural Biotechnology and Biochemistry (RLABB), GPO Box 8207, Kathmandu, Nepal*
[c] *Laboratory of Growth Regulation Chemistry, Department of Biological Production, Akita Prefectural University, Akita 010-0195, Japan*
[d] *Food Function Laboratory, School of Agriculture, Ibaraki University, Ami, Ibaraki 300-0393, Japan*
[e] *Department of Biotechnology, Agricultural Plant Stress Research Center, Biotechnology Research Institute,*
College of Agriculture and Life Sciences, Chonnam National University, Buk-gu, Kwangju 500-757, Republic of Korea
[f] *Human Stress Signal Research Center (HSS), National Institute of Advanced Industrial Science*
and Technology (AIST) WEST, Onogawa 16-1, Tsukuba, Ibaraki 305-8566, Japan

Received 5 October 2005
Available online 16 June 2006

Abstract

Rice, a first cereal crop whose draft genome sequence from two subspecies (japonica-type cv. Nipponbare and indica-type 93-11) was available in 2002, along with its almost complete genome sequence in 2005, has drawn the attention of researchers worldwide because of its immense impact on human existence. One of the most critical research areas in rice is to discern the self-defense mechanism(s), an innate property of all living organisms. The last few decades have seen scattered research into rice responses to diverse environmental stimuli and stress factors. Our understanding on rice self-defense mechanism has increased considerably with accelerated research during recent years mainly due to identification and characterization of several defense/stress-related components, genes, proteins and secondary metabolites. As these identified components have been used to study the defense/stress pathways, their compilation in this review will undoubtedly help rice (and others) researchers to effectively use them as a potential marker for better understanding, and ultimately, in defining rice (and plant) self-defense response pathways.

Keywords: Defense/stress response; *Oryza sativa*; Pathogenesis-related protein genes; Potential markers; Oxidative stress; Phytoalexins

1. Introduction

The grass family member rice (*Oryza sativa* L.) along with other important crop plant species, maize, wheat, barley, sorghum and sugarcane provide most of the world's food for human consumption and animals. If a single plant species were to be voted the most popular by scientists and laymen alike, it would be "rice" [35,135]. Rice is produced all around the globe from Nepal, which has the highest rice fields in the world, to Australia, which has the most productive rice lands [Rice Web, http://www.riceweb.org]. Rice (*O. sativa* ssp. japonica-type cv. Nipponbare and indica-type) is a model plant among the monocotyledonous cereal crop species based on the fact that rice i) has a relatively small genome of about 440 Mb (the maize genome is 2500 Mb, and that of barley 4900 Mb) [20], ii) is suitable for efficient genetic analysis and transformation [69], iii) draft genome sequence of both the japonica (cv. Nipponbare [58]) and indica (cv. 93-11 [169]) subspecies is available [32] along with the complete genome sequence [73], and iv) has high degree of homology with other cereal genes, where synteny rice and other cereals, especially with maize [32]. Therefore, rice becomes one of the

---

[*] Corresponding author.
E-mail address: rakwal-68@aist.go.jp (R. Rakwal).

[1] Present address: Biochemistry Department, University of Missouri-Columbia, 204 Life Sciences Center, Columbia, MO 65211, USA.

0981-9428/$ - see front matter © 2006 Elsevier SAS. All rights reserved.
doi:10.1016/j.plaphy.2006.06.010

most critical plant species to study and improve due to the constant threat of global climate change coupled with disastrous yield losses by “pest and pathogen” attack, and a rapid increase in the world’s population growth.

“Stress alleviation or disease control” remains one of the most challenging issues to be addressed, which is especially true for rice considering the largely undefined area of rice self-defense mechanisms. The hypersensitive reaction (HR), one of the most efficient (and visible) parts of the defense mechanisms in nature against invading pathogens [57,99] and/or stresses, is associated with a coordinated and integrated set of metabolic alterations which are instrumental in impeding further pathogen ingress or alleviating stress, and includes a variety of novel proteins (genes), and secondary metabolites. Active research on various aspects of defense/stress response in rice has resulted in the identification of a variety of response genes, proteins and antifungal secondary metabolites induced in response to diverse environmental stresses, including pathogen attack. These studies have provided novel insight into these responses and mark a major advance in our understanding on the rice self-defense mechanisms. These components are the responses of integrated signaling networks triggered under unfavorable circumstances, and hence they were assigned as a potential marker(s) based on their responses to a specific stimuli and/or multiple factors (Fig. 1). As these markers are intimately associated with a plant response to its environment, these marker genes, proteins, and secondary metabolites are of particular importance for studying the defense/stress pathways. Hence, the purpose of this review is to summarize the past and present progress made on this important aspect and discuss their usefulness in future studies in rice. It is emphasized here that we mostly deal with published articles in the literature databases (PubMed and ScienceDirect) and have included the genes, proteins and metabolites that have been experimentally demonstrated to be a part of the rice self-defense responses, in the current review. The availability of the rice genome sequence no doubt has increased the coverage of the rice genes homologous to known genes, but these remain to be functionally characterized and will be dealt in future studies.

2. Pathogenesis-related protein genes

Plant responses to attack by pathogenic microorganisms are complex, and involve the induction of expression of a large array of genes encoding diverse proteins, many of which are believed to have a role in defense/stress. Among these the production/accumulation of pathogenesis-related (PR) proteins in plants in response to invading pathogen and/or related stress situations [24,159] is one of the crucial components in the inducible repertoire of the plant’s self-defense mechanism, and used widely as marker genes/proteins to study the plant self-defense mechanism(s). The PR proteins were initially classified into 5 families based on molecular mass, isoelectric point, and localization and biological activity [159]. The latest proposition divides the currently known PR proteins into 14

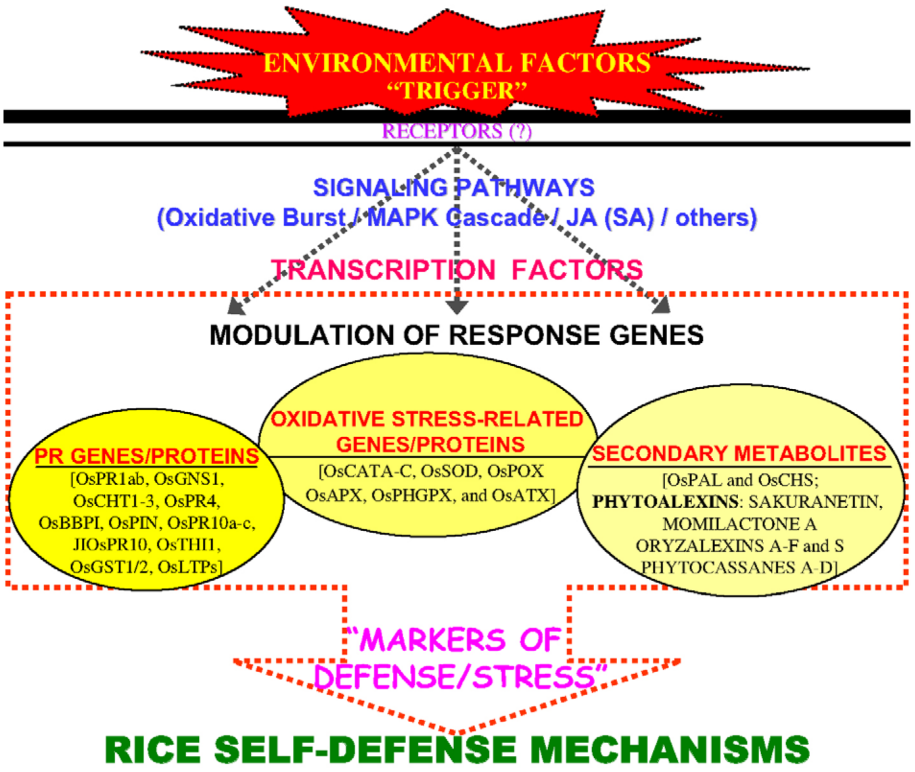

Fig. 1. Environmental factors triggering the rice self-defense mechanisms with a particular focus on endogenous markers involved in defense/stress responses. These components are the responses of integrated signaling networks triggered under unfavorable circumstances, and hence they were assigned as a potential marker(s) based on their responses to a specific stimuli and/or multiple factors.